STUDIES ON THE PHENOTYPIC MANIFESTATION OF HEREDITARY FACTORS. I. ON THE PHENOTYPIC MANIFESTATION OF THE GENOVARIATION RADIUS INCOMPLETUS IN *DROSOPHILA FUNEBRIS*

N. W. TIMOFÉEFF-RESSOVSKY

Institute of Experimental Biology, Moscow, Russia

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INTRODUCTION

This work was begun in the summer of 1923, at first as a simple genetic analysis of a newly appeared genovariation[1] in *Drosophila funebris.*

[1] I use the expression "genovariation" in the sense which Professor S. S. TSHETVERIKOFF gave to this term in his report made in February, 1924, at the meeting of the Zoological Section of O. L. E. A. and A., and which, some years before, he introduced in his paper, "The theoretical basis of systematics," read by him in the I Moscow University. This expression is substituted for the term "mutation," in the sense given the latter by MORGAN. The substitution of another term for the word "mutation" in all cases in which we have to deal with the apparition of a new gene is quite expedient, because the latter word is often used in quite different senses (in paleontology, mutations of DEVRIES, MORGAN's mutations). The term "genovariation" signifies that change of genotype which gives rise to a new gene, that is, it corresponds to the word "mutation" in the sense which MORGAN gave it.

During this analysis it became evident that the given genovariation had some peculiarities in its phenotypic manifestation. It also proved to be a very convenient object for the examination of some questions of theoretical genetics connected with the phenotypic manifestation of hereditary characters. Therefore the work was enlarged and continued according to a certain plan, with some peculiarities in the methods, which are explained in a later section.

The phenotypic manifestation of hereditary characters

If we consider hereditary characters from the point of view of their phenotypic manifestation we are enabled to classify them descriptively into three principal categories. To the first category belong those hereditary characters whose phenotypic manifestation is full and absolute. The second category is formed of those hereditary characters whose phenotypic manifestation depends upon the presence of definite external conditions, which either are favorable to the phenotypic manifestation of these characters or suppress it. In the third category are those hereditary characters which, though called forth by one gene, depend in their phenotypic manifestation upon internal hereditary conditions, or, in other words, characters whose degree of manifestation and of phenotypic expression is influenced by other genes.

To the characters of the first category belong all the recessive hereditary characters which never appear in the heterozygous and always appear in the homozygous state, usually more or less uniformly. The dominant characters belonging here are those which always appear in both the homozygous and heterozygous state; the degree of their phenotypic manifestation is more or less permanent, though it can be different in the heterozygous and homozygous conditions.

The characters of the second category appear only in the presence of definite favorable external conditions. We can give as an example here the dominant sex-linked genovariation abnormal abdomen in *Drosophila melanogaster*. According to MORGAN's investigations abnormal abdomen appears only in case of sufficient humidity of the food, whereas in dry cultures this character, even in its homozygous state, may not appear. According to the investigations of D. D. ROMASHOFF[2] the same facts can be observed in an analogous genovariation in *Drosophila funebris* which, though also dominant, is not sex-linked; the character appears only in case of sufficient humidity and nutritiousness of food. There are many

[2] The report was made at a colloquium in the INSTITUTE OF EXPERIMENTAL BIOLOGY in autumn, 1924.

examples of the same kind in *Drosophila melanogaster* as well as in a series of other species, among both dominant and recessive characters. By regulation of different external conditions, such as temperature, food and others, we can obtain different degrees of manifestation and phenotypic expression of such characters.

To the third category belong cases in which a gene, either dominant or recessive, manifests itself fully and clearly only in the presence of other definite genes, "intensifiers." If these supplementary genes are absent, the crucial gene appears less fully, and, in some cases, may not appear at all. Cases in point are, for example, the genovariations beaded, truncate and vortex in *Drosophila melanogaster*.

The above stated division of hereditary characters according to their phenotypic manifestation is, of course, a much simplified and schematized one. Very often the manifestation of the character does not depend so strongly upon definite external conditions as in the examples I mentioned, or, if this dependence exists, it does not affect the manifestation of the character so strongly, and therefore is not so perceptible. Often too we see combinations of the categories mentioned, that is, cases in which the manifestation of the character depends upon both external and internal condtions. A fine example of this last is the genovariation beaded in *Drosophila melanogaster*, the object of Professor MULLER's excellent investigation of balanced lethals.

The division given emphasizes certain aspects of the manifestation of hereditary characters and can serve as a basis for the study of their phenotypic manifestations and phenotypic expression.

Material and methods

Radius incompletus, the genovariation of *Drosophila funebris* which forms the object of this work, is recessive and autosomal. It finds its phenotypic expression in the absence of the distal end of the second longitudinal vein (radius) in the wings of flies homozygous for this geno-variation. The usual phenotypic expression of this genovariation is shown in figure 1.

Radius incompletus varies considerably in its phenotypic manifestation and expression. The amount missing from the distal end of the second longitudinal vein is highly variable. Figure 2 represents a high degree of phenotypic expression of this character in usual cultures. In addition to this, in some specimens, the part of the second longitudinal vein that is left may be broken off at the distal end. This form of expression of radius incompletus can also vary from case to case, as illustrated by the two

typical cases represented in figures 3 and 4. The character radius incompletus can, moreover, be manifested asymmetrically on the two wings, which may show differences from each other in both the degree and the form of its manifestations; in some cases one of the wings can be quite normal.
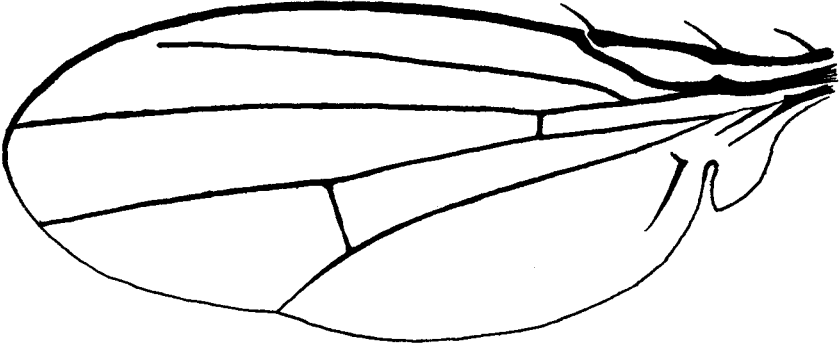
FIGURE 1

It can be seen further, from the statement about the material, that in some homozygous lines of this genovariation there may appear flies phenotypically normal in both wings.

To avoid unclearness, I wish to explain that I use the word "manifestation" to signify the presence of the given character in the phenotype of
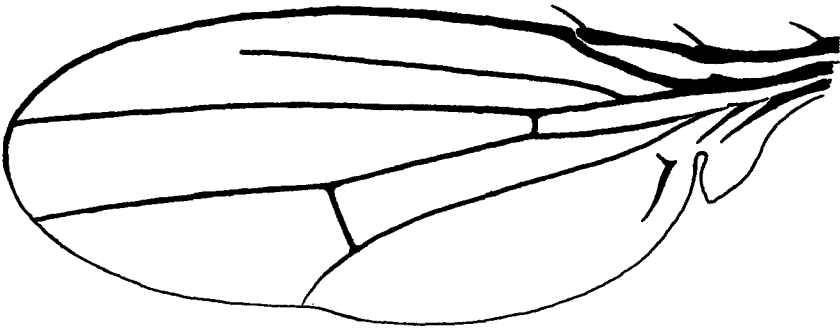
FIGURE 2

the fly, and the word "expression" to signify the degree and form of the character. In this work I did not ordinarily take into consideration the degree of expression of the character, but only the strongest changes in its expression, such as could be defined on sight. The principal object of this study was the degree of phenotypic manifestation of the character, that is, the percent of phenotypically normal flies in cultures homozygous for radius incompletus.

The cultures of flies were reared in small test bottles. The food was cooked as follows: to 100 gm of grated potatoes were added 20 gm of grated raisins, 1 gm of agar and about 250–300 cc of water. This food was put into the test bottles and some yeast poured in.

When summarizing the results of crosses I took into account only those test bottles in which the number of flies was normal, in consideration of
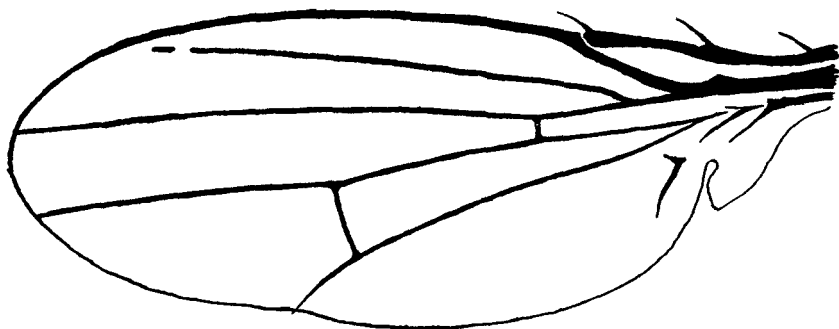
FIGURE 3

the size of the bottles. Thus mistakes were avoided that could otherwise have occurred if the conditions of existence and development of the flies in some cultures had happened to be abnormal, owing to some accident (such as mould, extreme drying, rotting or excessive fermentation of the food). Highly abnormal conditions in the test bottle may often alter the
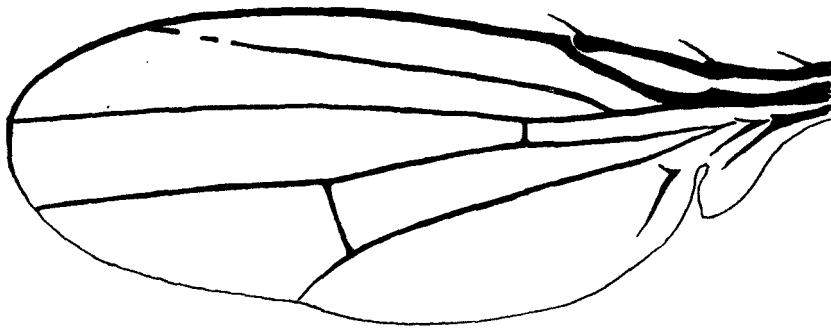
FIGURE 4

manifestation of a character as well as the normal numerical relation between different categories of flies expected to be in that test bottle.

It is also most important to avoid the excessive crowding of the test bottle with larvae. This condition causes an intensive natural selection between the different categories of flies, owing to which the less viable ones are hatched in smaller quantity. Thus, if we expect to have in a test bottle two or more different categories of flies, as happens in obtaining

Mendelian ratios, then the overcrowding of the test bottle may cause an abnormal relation between these categories. It is easy to avoid such overcrowding: one must not allow flies to lay eggs a long time in one test bottle, but remove the pair of flies from one test bottle to another. This also enables us to obtain a larger number of offspring from one pair.

The viability of radius incompletus is normal, as well as its fecundity being not inferior to that of normal flies. Notwithstanding this, the above-mentioned conditions of control and methods of crossing are not superfluous precautions in the work with radius incompletus.

I used for my work lines that were more or less pure, in that they were not only homozygous for the given factor, but had been inbred for 10 to 15 generations. Owing to this these lines were in great measure genetically homogeneous. This condition is very important in work concerning the phenotypic manifestation. or expression of a hereditary factor. Failure to fulfill it may be the cause of insufficiently clear results or of their incorrect treatment.

We have observed no definite external conditions, of those that can be observed in the ordinary rearing of cultures (temperature, humidity), that had any strong effect on the phenotypic manifestation of radius incompletus. It is very probable, nevertheless, that if we should make special precise investigations we would observe such effects; hence, it is very important to avoid any mistakes, in the making of crosses, such as might result from differences in external conditions in the different test bottles. These mistakes can be avoided by the summing up of a sufficient number of test bottles for each line; thus the differences will be levelled and we shall be enabled to compare different lines, considering the external conditions of rearing in all these lines as quite equal.

EXPERIMENTAL PART

The appearance of radius incompletus and the selection of the first three lines

The genovariation radius incompletus appeared in the summer of 1923 in the pure normal culture $L5_{II}-I$. This culture, which had been reared for biometrical purposes, originated from a wild population that lived at that time on rotten potatoes in one of the buildings near the Hydro-physiological Station of the INSTITUTE of EXPERIMENTAL BIOLOGY, in the Zvenigorodsky Department of the Moscow Government. At the time when the given genovariation appeared; the culture $L5_{II}-I$ had been inbred in our laboratories through 15 generations, we can therefore consider this culture as highly homogeneous and pure genetically. Radius incompletus appeared in one of the test bottles of this line, and there were

three specimens of it—one female and two males. The three specimens bore the character on both wings, but it was slightly marked, in nearly the same degree as represented in figure 1. The radius incompletus female was crossed with one of the radius incompletus males, but unfortunately they perished without giving any progeny.

The second radius incompletus male was crossed with a normal female from a related normal pure line, $L5_{II}$–II. This normal culture originated from the same pair of flies as the culture $L5_{II}$–I.

Flies of the first generation of this crossing, marked N 16, were all normal. In the second generation a splitting occurred: 73 flies were normal and 21 radius incompletus. These numbers are approximately the same as those expected for the monohybrid splitting, namely 70.5N: 23.5r.i. We must recognize this genovariation as being an autosomal one, that is, not linked with sex, because among the radius incompletus flies there were females as well as males. This will be confirmed by a series of further crossings.

A pair of normal-appearing flies, which had been taken from culture $L5_{II}$–I, from the same generation in which radius incompletus appeared, were also mated together, and this cross was designated as N 14. Besides, there had been taken, from the same generation, a normal male and crossed with a normal female, from an unrelated, wild, mixed culture, and this cross was marked N 13.

All these crosses are to be seen in diagram 1.

In the first generation of the crossing N 14 all the flies were normal. But in the second generation which came from one pair of the first generation there occurred a splitting, which gave 42 normal flies and 13 radius incompletus flies. This shows that one of the original flies of this cross was heterozygous for radius incompletus, and that the two flies which had been taken to get the second generation were by accident both heterozygous for the same gene.

Cross N 13 showed that the male fly from $L5_{II}$–I also had been heterozygous for radius incompletus. In the first generation of this cross all the flies were normal, but in the second generation there occurred 70 normals and 24 radius incompletus.

These three crosses show the usual rising up of a recessive genovariation. At first there appeared only one heterozygous specimen, which further on gave in culture $L5_{II}$–I more flies heterozygous and homozygous for radius incompletus.

We obtained from the radius incompletus flies of the second generation of these crosses, through further inbreeding, three lines which were homozygous for radius incompletus, and kept for these lines the numbers of the original crosses.

Line N 14 was a pure line from the beginning, for the inbreeding was not once broken off. The other two lines, 16 and 13, were inbred through a series of generations, so that they also can be considered as being more or less pure.

It was observed during the further rearing of these three lines that the phenotypic manifestation of radius incompletus is the same in lines N 14 and N 16 and different in line N 13. Lines N 14 and N 16 always give some normal flies, notwithstanding the fact that they are extremely homozygous in their genetic nature, having been inbred through a large number of generations. Line N 13 "purified itself" almost immediately and gave further only such flies as had the radius incompletus character clearly manifested.

The normal flies of lines N 14 and N 16 were only phenotypically normal, because in their progeny as well as in the progeny of the radius incompletus flies of these lines, the percent of phenotypically normal specimens was approximately the same.

The phenotypic manifestation of radius incompletus in lines N 14 and N 16 was partly sex-limited in a way quite visible to us. In general this character is expressed in males in a stronger degree than in females; the most strongly expressed radius incompletus is met with among males, and the slightest degree of expression is met with among females. It strikes the eyes that the phenotypically normal flies are mostly females.

Crosses that characterize lines N 14, N 16 and N 13 are shown in tables N 1–N 5.

The numbers of the radius incompletus and of the phenotypically normal flies in five cultures of line N 14 are given in the table N 1. Out of the total number, 1194 flies, 1073 manifested the radius incompletus character and 121 were phenotypically normal. The rate of phenotypically normal flies for line N 14 is, in comparison with the total number of specimens, 10.13 percent. (It should be noticed that in each case the percentages of the phenotypically normal flies are calculated in relation to the total number, not in relation to the number of radius incompletus flies.)

The numbers of radius incompletus and phenotypically normal flies of line N 16 are to be found in table 2. The sum total of specimens in five cultures is 1259, among which are 1128 radius incompletus flies and 131 phenotypically normal. This makes 10.41 percent of phenotypically normal flies in that line.

According to their percents of phenotypically normal flies, lines N 14 and N 16 do not differ from one another. But this does not mean that they

are identical, for, as will be shown in one of the following paragraphs, there were obtained from crosses between flies of these two lines a heterogeneous progeny from which by selection new lines were gotten, that differed from the original lines in their percent of phenotypically normal flies.

In table 3 we see the summing up of the five cultures of line 13. Here, among 1155 flies, there appeared only 3 phenotypically normal ones. Two normal flies of the second culture from this table, and their progeny, after being inbred for four generations, gave 679 radius incompletus flies and not a single normal one. The results of the crossing with the normal fly of the fifth culture in this table will be given in one of the following paragraphs. We can consider line N 13 as one giving 100 percent of manifestation of radius incompletus.

Table 4 shows the percent of phenotypically normal flies in the progeny of radius incompletus and phenotypically normal parents of the lines N 14 and N 16. In the progeny of radius incompletus flies of the line 14 we obtained 10.30 percent of normal flies and in the progeny of phenotypically normal ones in the same line 10.52 percent. The difference between these numbers is not significant. The same happened in line 16, where the phenotypically normal flies in both cases are equal to 10.60 percent and 10.53 percent. This difference also is not significant.

All the above mentioned facts are highly essential. First of all they show that the manifestation of radius incompletus is in various lines, that is, in various genotypes, different. In lines N 14 and N 16 the manifestation is not complete, in line N 13 it is complete. Secondly, they show the following facts: on the one hand, the different manifestation of radius incompletus in different lines shows the dependence of the phenotypic manifestation of this character upon one or another genotype; on the other hand, in lines N 14 and N 16, which are more or less genetically homogeneous (line N 14 was closely inbred through 30 generations) a part of the flies did not manifest the radius incompletus characters. This non-manifestation is purely phenotypic, and taking into consideration the absence of influence of external conditions on the manifestation of this character, we can consider it as characteristic for a certain genotype to have a certain percent of phenotypic manifestation of radius incompletus.

The degree of sex-limitation of the phenotypic manifestation of radius incompletus in lines N 14 and N 16 is to be seen in table 5. Here the percent of phenotypically normal flies is calculated separately for males and females. There is, in line N 14, 16.49 percent of phenotypically normal flies among females and 4.34 percent among males. In line N 16 the pheno-

typically normal females form 16.28 percent and the phenotypically normal males 4.22 percent. Both these lines show a certain sex-limitation—in males radius incompletus is more easily manifested than in females.

Flies of the radius incompletus lines N 14, N 16, and N 13 were crossed with normal flies of two different normal pure lines. One of these lines is designated as L 5—it is connected with the line that gave rise to radius incompletus. The second normal pure line is marked K II and comes from "Gaspra", a place in Crimea. During our whole work these two lines, L 5 and K II, were standard normal pure lines used for crossings with different radius incompletus lines.

All three radius incompletus lines give in the first generation of the crossing with line L 5, as well as with line K II, only normal flies, that is, they are quite recessive, and in the second generation a splitting occurs.

In tables 6 to 8 numbers are given for the second generations of crosses between radius incompletus lines N 14, N 16, and N 13, and the normal line L 5.

In tables 9 to 11 numbers are given for the second generations of crosses between the same radius incompletus lines and the normal line K II.

A real deviation from the expected 3:1 ratio was given only by the cross between radius incompletus N 14 and the normal line K II (3.66 ±0.21:1.0), and the cross of radius incompletus N 16 with the same normal line K II, which gave 3.76±0.21:1.0. The other crosses gave at the summing up no significant deviation from the expected 3:1 ratio.

In most cases the ratios obtained in the second generation of crosses between different radius incompletus lines and normal cultures are within the limits of probable error, both in comparison with one another and in comparison with the expected Mendelian 3:1 ratio. The deviations are usually so small, that to establish their significance it would be necessary to obtain an extremely large number of flies from different crosses. This can be explained by the fact already mentioned, that the radius incompletus flies possess quite a normal viability, and a strong deviation from the expected 3:1 ratio is usually the result of the low viability of flies homozygous for some recessive genovariations.

The effect of some external conditions on the manifestation and viability of genovariations can alter the Mendelian ratio or provoke considerable fluctuations in it. In our work, however, this did not happen, for external conditions which can be met with in the usual cultures do not alter so strongly either the manifestation or the viability of radius incompletus.

The differences in the Mendelian ratios obtained in crossings of different radius incompletus lines with normal cultures L 5 and K II, although they are not quite "significant," have, together with other genetical conditions of these lines, an importance for the characterization of radius incompletus lines. Evidently these deviations are to some extent connected with a definite percent of non-manifestations of the character in individuals homozygous for radius incompletus. The importance of these deviations from the 3:1 ratio will be more apparent later, after a series of different lines and crosses have been noted.

Obtaining the next five lines and their nature

As the above-mentioned lines made it evident that the chief radius incompletus gene is manifested in various genotypes in different degrees, I next made up further radius incompletus lines, obtaining them generally from the second generation of crossings between radius incompletus and normal flies of different origin. These lines were inbred through 10–15 generations and then investigated in the same manner as the first three lines, that is, the percent of phenotypically normal flies in them was calculated and crossings were made with the pure normal lines L 5 and K II.

a. Line N 173

Line N 173 was obtained from the cross between the phenotypically normal male which appeared in radius incompletus line 13 and his sister. This male has already been mentioned; he is the single normal specimen among 237 flies of the fifth culture in table 3.

The diagram 2 shows the results of the cross.

Line N 13, as was stated in the preceding paragraph, gives 100 percent of manifestation of radius incompletus. In the first generation of this cross, among a total of 131 flies, five proved to be normal. To obtain the second generation we took three pairs of flies—one radius incompletus pair and two pairs from among the five phenotypically normal specimens of the first generation. The radius incompletus pair gave as its progeny all radius incompletus flies. The two generations following this also gave the same results.

In the progeny of the two phenotypically normal pairs there appeared a certain number of phenotypically normal flies in each of the following generations. The line derived from one of these pairs was soon broken off and the second line, derived from the other pair, was left as line N 173.

After the line N 173 had been inbred through 8 generations (the inbreeding had not been broken off from the foundation of line N 13) there

were obtained in one of the generations a great number of flies, and the percent of phenotypically normal flies for this line was then calculated. The results are to be found in table 12. Line N 173 gives 14.89 percent ±0.85 percent of phenotypically normal flies.

Flies of this line were crossed with flies of the radius incompletus line N 13. In the first generation there were obtained only radius incompletus flies. In the second generation of these crosses there appeared about 4 percent of phenotypically normal flies. In table 13 we see the numbers obtained in the second generations of five similar crosses. Among 623 flies 25 proved to be phenotypically normal, that is, 4.01 ±0.80 percent.

In the first generation of the cross between flies of line N 173 and flies of the normal culture K II only normal flies were obtained. In the second generation a splitting occurred, the results of which are given in table 14. The ratio 3.52 ±0.27:1 was obtained.

It is quite probable that in the radius incompletus line 13 a gene arose which changed the manifestation of the radius incompletus character, and the purification of the culture in respect to this gene gave rise to line N 173. The origination of the line N 173 from the pure culture N 13 serves as an indication of this, as well as the results of crosses between flies of these lines, because in the second generation of such crosses the normal flies appear in a quantity that is four times smaller than that of line N 173.

b. Line 81

One female of the pure radius incompletus line N 16 (which gave about 10 percent of phenotypically normal flies) was crossed with a wild male from the Zvenigorodsky Department of the Moscow Government. In the first generation of this crossing, among 73 flies obtained, 3 proved to be radius incompletus. Among these three specimens one was a female and the other two males. To obtain the second generation we crossed one pair of normal and one pair of radius incompletus flies from the first generation. In diagram 3 we can find these crossings.

In the second generation, in the progeny of the normal parents, among 87 flies 22 bore the character radius incompletus, and, in the progeny of the radius incompletus parents, among 90 flies 23 were radius incompletus. With the radius incompletus flies of these two branches several crosses of flies homozygous for radius incompletus were carried out, as can be seen in diagram 3. In the further generations a part of these crosses gave a certain percent of phenotypically normal flies. One of the lines (on the right edge of the diagram) which was derived from the radius incompletus pair of the first generation, on being inbred through many generations

gave always only well expressed radius incompletus specimens; phenotyp-
ically normal flies did not appear. All the other lines were broken off.

Having inbred line N 81 through ten generations we investigated that
line in the same way as the preceding ones.

Table 15 shows that, among 1178 flies obtained from one generation
of the line N 81, only one fly proved to be normal. This was a female, and
for the sake of verification she was crossed with her brother, but this
cross perished without giving any offspring.

Flies from radius incompletus line N 81 were crossed with normal flies
from line L 5. In the first generation of all such crosses a certain percent
of radius incompletus flies appears.

Table 16 shows that, among 747 flies of the first generation of these
crosses, 45 flies proved to be radius incompletus, that is, we have 6.02
percent of manifestation of this character in the first generation. In these
radius incompletus flies the character is usually expressed in a very slight
degree and in some individuals radius incompletus is manifested asym-
metrically.

To obtain the second generation normal and radius incompletus flies
of the first generation were crossed with one another separately.

In table 17 the results of the splitting in the progeny of radius
incompletus flies of the first generation are to be seen. The ratio obtained
here is $2.96 \pm 0.20 : 1$.

In table 18 there is shown the splitting in the progeny of normal
flies of the first generation. The ratio obtained is $2.92 \pm 0.19 : 1$.

The normal and the radius incompletus flies of the first generation
give a similar ratio in the second generation. This was to be expected
because both lines—N 81 and L 5—are more or less pure, and the first
generation therefore must be genetically homogeneous.

Thus it is seen that line N 81 in the crossing with line L 5 shows an
incomplete dominance, which can be expressed in terms of the percent
of radius incompletus flies obtained in the first generation. Evidently the
manifestation or the non-manifestation of the character in the first
generation of these crosses does not depend upon a genetic difference
between single individuals of the first generation, for all this generation
is homogeneous in its genetical nature. The genotype, in this case the
genotype of the first generation, calls forth a definite percent of mani-
festation of this character, as we have already seen in the pure homozygous
radius incompletus lines N 14, N 16 and N 173.

For crossings of the radius incompletus line N 81 with normal Crimean
flies we did not take the pure line K II but took a mass culture of the same
population K II, that is, a heterogeneous culture.

Table 19 shows the results obtained from the first generation of the cross between line N 81 and the mass culture K II. A partial dominance was obtained, 5.17 percent of the flies manifesting the character radius incompletus.

Tables 20 and 21 show data for the second generations obtained from normal and radius incompletus flies of the first generation.

Thus line N 81 gives in the pure culture 100 percent of manifestation of radius incompletus and shows a slight dominance over the normal cultures L5 and K II.

c. Line N 180

In diagram 4 is shown the origin of line N 180. A radius incompletus female derived from the cross between radius incompletus of line N 16 and radius incompletus of line N 14 (both these lines give about 10 percent of phenotypically normal flies) was crossed with an Alae divergentes (a dominant genovariation with spread wings, lethal in homozygous condition) male, heterozygous for radius incompletus. In the first generation of this cross 18 Alae divergentes and 21 radius incompletus flies appeared. A line homozygous for radius incompletus was formed from these radius incompletus flies, and in the first generation of this culture 66 radius incompletus flies and 3 phenotypically normal ones appeared.

As can be seen in the diagram, a selection in two different directions was started from that generation on. The selection was effected by inbreeding and led to the formation of two lines, one of which gave a complete manifestation of the radius incompletus character and the other gave about 12 percent of phenotypically normal flies. The line which gave 100 percent of manifestation, after being inbred through 11 generations, was investigated in the usual way.

In table 22 we can see that among 1203 flies, in one of the generations of this line, only one phenotypically normal fly appeared. It was a male which did not bear the radius incompletus character, but his wings were of a different size, the left one being shorter than the right one. Besides this he was very small, feeble and inactive. In spite of the fact that several females were by turns put into his test bottle, he did not fecundate them and gave no progeny.

The crosses between radius incompletus flies from the line N 180 and normal flies from line L 5 gave the following results. In the first generation of these crosses, this line, like the line N 81, showed a slight dominance. Table 23 shows that radius incompletus appeared in the first generation in 5.18 percent of cases. From tables 24 and 25 we can see that in the second generation the splitting in the progeny of radius incompletus

flies was identical with that in the progeny of the normal flies of the first generation, and that it was besides very near to the 3:1 ratio.

Tables 26, 27 and 28 show the results of the crosses between radius incompletus N 180 and the pure normal line K II. In the first generation of these crosses the dominance is expressed by 6.96 percent of radius incompletus manifestation. In the second generation the splitting is identical both in the progeny of normal and of radius incompletus flies of the first generation, for the two lines—N 180 and K II—were more or less pure.

Line N 180 is seen to be similar to line N 81, both in giving 100 percent of manifestation of radius incompletus and in showing incomplete dominance over the normal lines L 5 and K II, approximately in 5–6 percent of cases. But these two lines differ from one another in the degree of the phenotypic expression of the radius incompletus character. Flies of the line N 81 show a strong degree of expression of radius incompletus, whereas in line N 180 the expression of radius incompletus is of the usual degree. Not in one of the above-mentioned lines did the character occur so strongly expressed as in line N 81. Besides, as will be seen in one of the following paragraphs, the genotypes of these two lines are not identical.

d. Line N 192

Diagram 5 shows the origin of the line N 192 and the means of its purification. A radius incompletus female of the mixed mass culture N 173 was crossed with a male of a mixed normal mass culture. In the second generation a splitting occurred which gave 78 normal and 19 radius incompletus flies. From these radius incompletus flies a homozygous culture was raised, in the first generation of which 91 radius incompletus flies and 18 phenotypically normal ones appeared. To obtain further generations we took one pair of the phenotypically normal flies in each generation. This line had been inbred in this way through 10 generations, when it was investigated in the usual manner.

Table 29 shows the percent of phenotypically normal flies in the progeny of the radius incompletus and of normal parents of this line. In both cases the percent is equal. Line N 192 gives about 16 percent of phenotypically normal flies.

In table 30 the results of the splitting in the crosses between line N 192 and the pure normal line K II are given. The ratio $3.82 \pm 0.22:1$ was obtained; this differs significantly from the expected 3:1 ratio. Evidently this difference was caused by the non-manifestation of a part of the homozygous radius incompletus in the second generation. It occurred

several times that normal flies from the second generation of these crosses proved to be homozygous for radius incompletus.

Only one cross was arranged with line L 5; the number of flies obtained are so small that they have no importance in our comparisons.

e. Line N 205

This line was obtained by crossing radius incompletus from line N 81 with radius incompletus from line N 180. Its origin can be seen in diagram N 6. In the first generation of the crossing between a radius incompletus female of line N 81 and a radius incompletus male of line N 180, 83 flies were obtained among which there was not a single phenotypically normal fly. Three pairs of flies were crossed to obtain the second generation. In all the three crosses there appeared some phenotypically normal flies. Further, beginning with the cross represented on the left side of the diagram, an inbreeding was carried on, for which purpose a pair of radius incompletus flies was taken in each generation. After being inbred thus through several generations the line gave 100 percent of manifestation of radius incompletus; it was investigated after the 10th generation.

The summing up of flies in one of the generations of line N 205, after its purification, is given in table 31. Among 1192 flies only two proved to be normal. These were very small females which folded their wings in a way that resembled a roof, that is, the front edges of the wings were lowered and close to the sides of the body. Their abdomen was deformed, being very narrow in the posterior and swollen in the anterior region. These females gave no offspring although different males were put into their test bottles. One of these females was dissected and it was discovered that the ovaries and the receptaculum seminis were abnormal and insufficiently developed. Evidently this sterile alteration affected the manifestation of radius incompletus.

In the first generation of the crosses between line N 205 and the normal line L 5 a slight dominance was observed. It can be seen from table 32 that the radius incompletus character manifested itself in the first generation in 4.38 percent of flies. In the second generation the splitting in the progeny from the normal flies of the first generation is equal to that from the radius incompletus flies. The numbers obtained in these splittings are shown in tables 33 and 34.

The results obtained from the cross of radius incompletus N 205 with the pure normal line K II are different from those obtained before. In the first generation no dominance is obtained. It can be seen in table 35 that among 599 flies of the first generation only two flies proved to be

radius incompletus and the character was expressed only in a slightly perceptible degree. Table 36 shows the ratio obtained in the second generation.

Line 205 is very interesting in its origin. It was obtained as a result of the crossing of two "strong" radius incompletus lines—N 81 and N 180. The crossing of these two "strong" lines, as can be seen in diagram N 6, gave rise to two lines—to one "feeble" line giving constantly some percent of phenotypically normal flies and not dominating over lines L 5 and K II, and to the line N 205. The line N 205 differs from lines N 81 and N 180 in its genetical constitution. It dominates over the normal line L 5 only. In the degree of expression of radius incompletus this line is equal to line N 180; it does not give such a strong expression of the character as line N 81.

Selection of "feeble" and "strong" radius incompletus lines

Some more radius incompletus lines, obtained from different crosses, will be described in this section.

I designate by the word "feeble" those lines that give an incomplete manifestation. In addition, these lines are usually quite recessive, and often give in splittings deviations from the 3:1 ratio, which are not always significant, but nevertheless can be added to the characterization of these lines.

"Strong" lines always give a complete manifestation and several give also an incomplete dominance in crosses with certain normal lines.

a. "Feeble" radius incompletus lines

These lines were obtained by crosses between radius incompletus flies and normal ones. From the second generation of such crosses a homozygous culture was raised, and continued by the aid of inbreeding between phenotypically normal flies. Thus from the given culture a genotype could be obtained which would be the least favorable one for the manifestation of radius incompletus.

The obtaining of four "feeble" lines, "A," "B," "C" and "D" is to be seen in diagram 7.

Line "A" was obtained from the second generation of the cross between a radius incompletus female of line N 13 (100 percent of manifestation) and a normal male of the mass Crimean culture. This line had been inbred through 12 generations and afterwards investigated. Among the 2178 flies, obtained in the 12th generation, 1457 proved to be radius incompletus flies, and 721 phenotypically normal ones. This makes 33.10 percent of phenotypically normal flies. The cross between flies of this

line and normal flies of line L5 gave in the first generation only normal flies and in the second generation, among 1068 flies, 847 proved to be normals, and 221 radius incompletus; this gives a 3.83:1 ratio. The cross of radius incompletus "A" with normal flies of line K II gave in the first generation only normal flies and in the second generation 241 radius incompletus flies and 858 normal ones, that is, a 3.56:1 ratio.

Line "B" arose from a cross between a radius incompletus female of line N 13 and a normal wild male from the Zvenigorodsky Department of the Moscow Government. A homozygous line was reared from the radius incompletus flies of the second generation of this cross; this line, like line "A," was inbred through many generations, for which purpose a pair of phenotypically normal flies was taken from each generation. In the 12th generation of this line 784 radius incompletus flies and 186 phenotypically normal ones were obtained; this makes 19.12 percent of phenotypically normal flies in line "B." The cross between flies of these lines and normal flies of line L 5 gave in the first generation only normal flies, and in the second generation 494 normal flies and 145 radius incompletus flies, that is, a 3.42:1 ratio. The crosses with normal flies of line K II gave in the first generation only normal flies and in the second generation 132 radius incompletus flies and 488 normal ones, that is a 3.69:1 ratio.

Line "C" was obtained from a cross between a radius incompletus female of line N 13 and a normal male of the mass Crimean culture. The process of selection was the same as with lines "A" and "B." In the pure culture this line gave 9.68 percent of phenotypically normal flies (801 radius incompletus flies and 88 phenotypically normal ones). In the cross with normal line L 5, in the first generation all flies proved to be normal and in the second generation a splitting occurred which gave a 3.43:1 ratio (432 normal flies and 126 radius incompletus flies). In the cross with normal line K II in the first generation all flies proved to be normal in the second generation a splitting occurred which gave a 3.29:1 ratio. (137 radius incompletus flies and 451 normal ones.)

Line "D" was obtained from a cross between a radius incompletus female of line N 13 and a normal male from a mixed mass culture, in the same way as the preceding lines, "A," "B" and "C." In the pure culture this line gave 6.22 percent of phenotypically normal flies (919 radius incompletus flies and 61 phenotypically normal ones). The cross with line L 5 gave in the first generation only normal flies, and in the second generation a splitting in the form of a 3.19:1 ratio (694 normal flies and 217 radius incompletus flies). The crosses with line K II gave a feeble

dominance; in the first generation 191 normal flies and 11 radius incom-
pletus flies were obtained. In the second generation a 3.04:1 ratio was
obtained (635 normal flies and 209 radius incompletus flies).

It must be noticed that the radius incompletus females which are the
progenitors of this culture were taken from the pure line N 13, and there-
fore are more or less homogeneous. The normal males taken as generators
of these lines are genotypically different. The origination of several lines
differing one from another in their phenotypic manifestation of radius
incompletus is the result of crossings of one genotype, including radius
incompletus, with different normal genotypes.

b. "Strong" radius incompletus lines

These lines, like the "feeble" ones, were obtained from different crosses
between radius incompletus and normal flies. But the process of selection
of these cultures from the second generations of these crosses is different.
To obtain each next generation, this time a pair of radius incompletus
flies was taken, while before we took phenotypically normal ones.

The selection of the "strong" lines is to be seen in diagram 8.

Lines N 81 and N 180 have been already described (diagrams 3 and 4,
tables 15–28) and are mentioned here only for comparison with the other
three lines of diagram 8, for they were obtained in the same way. It may
be recalled that lines N 81 and N 180 give 100 percent of manifestation
of radius incompletus and reveal an incomplete dominance in the crossings
with normal lines L 5 and K II.

Line N 111 was obtained from a cross between a radius incompletus
female of line N 14 (10 percent of phenotypically normal flies) and a
normal male from a mixed mass culture. For four generations which
were homozygous for radius incompletus, this line gave a certain quantity
of phenotypically normal flies, but beginning with the fifth generation
it gave only radius incompletus flies. In the first generation of the cross
between this line and normal flies of line L 5, not even a single radius
incompletus fly appeared, but in the second generation of this cross a
splitting occurred which gave 219 radius incompletus flies and 665 normal
ones, that is, a 3.03:1 ratio. The crossing with line K II also gave in the
first generation only normal flies, and in the second generation a splitting
occurred in a 3.18:1 ratio (768 normal flies and 241 radius incompletus
flies). This line thus gives 100 percent of manifestation of radius incom ·
pletus, but is recessive in relation to lines L 5 and K II.

Line N 130 was obtained from a crossing between a normal female of
the Crimean mass culture and a radius incompletus male of line N 13.

In the first five generations of this line, when it became homozygous for radius incompletus, some phenotypically normal flies appeared. Beginning with the sixth generation this line gave only radius incompletus flies. The crossing with line L 5 gave in the first generation only normal flies and in the second a 3.16:1 ratio (734 normal flies and 232 radius incompletus flies). The cross with line K II also gave in the first generation only normal flies and in the second generation a 3.03:1 ratio (385 normal flies and 127 radius incompletus flies).

Line N 116 arose from the second generation of a cross between a normal female of a normal mixed mass culture and a radius incompletus male of line N 16 (10 percent of phenotypically normal flies). After becoming homozygous this line gave only radius incompletus flies, beginning with the fifth generation. In the first generation of the cross with L 5 only normal flies appeared and in the second generation a 3.04:1 ratio was obtained (518 normal flies and 167 radius incompletus flies). The crossing with line K II gave in the first generation 302 normal flies and 13 radius incompletus flies, and in the second generation a 3.24:1 ratio (464 normal flies and 143 radius incompletus flies). This line thus gives 100 percent of manifestation of radius incompletus and reveals a partial dominance over the line K II.

Crossings between several radius incompletus lines and the effect of selection in the pure and heterogeneous radius incompletus lines

To prove that some radius incompletus lines similar to one another in many of their characters and in their breeding behavior are not genotypically identical, crosses were made between these lines.

The cross between radius incompletus of line N 81 and radius incompletus of line N 180 has been represented in diagram N 6. Two new lines were obtained from this cross, line N 205, which has been mentioned previously, and another line, which gave about 9 percent of phenotypically normal flies and was quite recessive. This cross shows clearly that the genotypes of the lines N 81 and N 180 are not identical.

In diagram 9 the cross between radius incompletus of line N 13 (100 percent of manifestation and complete recessiveness) and radius incompletus of line N 16 (10 percent of phenotypically normal flies) is represented. From the second generation of this cross a selection was conducted in two directions, which led to the formation of two new lines. One of these lines gave, like line N 13, 100 percent of manifestation of radius incompletus, but revealed an incomplete dominance over the line

K II, a fact that never was observed in line N 13. The other line gave about 15 percent of phenotypically normal flies, that is, proved to be more "feeble" than the "feeble" parent, line N 16.

Diagram 10 shows the cross between two "feeble" lines. A radius incompletus female of line N 14 (10 percent of phenotypically normal flies) was crossed with a radius incompletus male of line N 16 (10 percent of phenotypically normal flies). The selection was continued in two directions. A line giving 100 percent of manifestation of radius incompletus was obtained, and at the same time another line, giving 14 percent of phenotypically normal flies.

In diagram 11 another cross between two "feeble" lines is represented. A radius incompletus female of line N 14 was crossed with a radius incompletus male of line "C" (9 percent of phenotypically normal flies). The selection was carried on in two different directions. The selection of radius incompletus flies led to the formation of a line which gave in its sixth generation 100 percent of manifestation of radius incompletus. Sometimes flies of this new line, in crossings with different normal flies, gave in the first generation flies with feebly expressed radius incompletus, that is, this line was able to dominate in a feeble degree. The selection of phenotypically normal flies led to the formation of a line which gave about 15 percent of phenotypically normal flies. Besides, as can be seen in diagram 11, from the fourth generation of this line a selection of radius incompletus flies was begun which led to the formation of a line giving 5 percent of phenotypically normal flies. Thus three new lines were obtained from the cross between lines N 14 and "C," which differed from one another and from the original lines.

In addition to the above-mentioned crossings, experiments were carried out to investigate the effect of selection in a heterogeneous mass culture homozygous for radius incompletus, and in the pure radius incompletus line N 14.

In diagram 12 the selection in the mass culture N 136 is to be seen. This selection led to the formation of two new lines, one giving 100 percent of manifestation of radius incompletus and the other giving about 9 percent of phenotypically normal flies.

The selection in the pure radius incompletus line N 14 is to be seen in diagram N 13. The selection continued through seven generations did not affect perceptibly the manifestation of radius incompletus.

All the crossings mentioned in this paragraph confirm the idea that differences in the phenotypic manifestation of radius incompletus in different lines are due to differences in the genotypes of these lines.

*Single genes affecting the phenotypic manifestation and
expression of radius incompletus*

In this paragraph there will be described cases in which some sort of
effect on the phenotypic manifestation and expression of radius incom-
pletus can be ascribed to a definite gene, or connected with a certain
character.

All the above-stated facts prove that the manifestation and expression
of radius incompletus can be affected by different genotypes into which
this gene is introduced. In most cases, all these hereditary differences
in the manifestation and expression of radius incompletus are evidently
polyhybridous and connected with different combinations of a large
number of genes. These facts are proved by the obtaining in abundance
of genetically different lines, and by crossings between these lines.

The effect on the manifestation and expression of radius incompletus of
four different genes, as well as of two hereditary characters the genetical
structure of which is as yet insufficiently determined, was revealed during
this work.

a. The "inhibitor" of culture N 163

In the pure radius incompletus culture N 13 which does not give any
phenotypically normal flies, there appeared a normal male. He was
crossed with his radius incompletus sister (cross 163). This cross is to be
seen in diagram N 14. In the first generation 58 radius incompletus flies
were obtained. In the second generation 86 flies were obtained, among
which 5 were phenotypically normal. From these phenotypically normal
flies line N 163 was established, which continued to give a certain quantity
of phenotypically normal flies. The summarizing of the flies in the
progeny of radius incompletus parents as well as in the progeny of normal
parents of this line is given in table 37. In both cases there is about 24
percent of phenotypically normal flies.

Diagram 15 shows the cross between radius incompletus of line N 13
and radius incompletus of line N 163. As can be seen in diagram 14,
line 163 represents the prolongation of the inbreeding in line N 13; it was
never mixed with another genotype, and the only difference lies in the
appearance of the normal male, the generator of line N 163. In the first
generation of the cross between lines N 13 and N 163 only radius incom-
pletus flies appear, but in the second generation a certain quantity of
phenotypically normal flies appear. In table 38 is given the summing
up of the first generation, and in table 39 the summing up of the second
generation of these crosses. Sufficiently large numbers reveal that in

line N 163 the number of phenotypically normal flies is four times as
large as in the second generation of these crosses. This fact can be ex-
plained as follows: the fourth part of flies of the second generation,
homozygous for a gene which provokes the non-manifestation of radius
incompletus in some flies in line N 163, gives, as in line N 163, about
24 percent of phenotypically normal flies; in relation to the total number
of flies in the second generation this gives about 6 percent of non-mani-
festation of radius incompletus. The results shown in tables 37, 38 and
39, as well as the method of origination of this line, confirm such an
explanation.

b. The "intensifier" of culture N 13

In one of the generations of a branch of radius incompletus line N 13,
52 flies were obtained, 43 of which had the character radius incompletus
expressed in an unusual degree, but in 9 flies radius incompletus was
expressed in an extremely strong degree—a half of the radius missing.
Among these 9 specimens were males and females. One of these males
as well as one of the females were respectively crossed with a male and a
female of culture 13. The origin of these flies as well as the above-
mentioned crosses are to be seen in diagram 16.

In the first generation of these crosses all the flies proved to be radius
incompletus, and in the second generation a splitting occurred which
gave in one of the crosses 52 flies with the usual expression of radius
incompletus and 14 flies with strongly expressed radius incompletus;
in the other cross 41 ordinary radius incompletus and 12 strongly expressed
radius incompletus flies were obtained. The further inbreeding of these
strongly expressed radius incompletus gave cultures with the same high
degree of expression of this character; this can be seen in the same dia-
gram, 16.

Crosses of these strongly expressed radius incompletus with normal
flies are to be seen in diagram 17. These crosses give quite a satisfactory
dihybrid splitting, though in this case it is not so easy to discriminate
between the usual degree of expression of radius incompletus and a strong
one, because the variety of degrees of expression is here greater than in
the pure line N 13.

All the above-mentioned facts show that this change is connected with
a gene, evidently not linked with the radius incompletus gene.

It was intended further to introduce this gene into different radius
incompletus lines, but all the cultures of this gene, as well as many others,
perished in the summer of 1924, because of an accidental raising of the
temperature up to 40° in the place where they were kept.

c. An inheritable sterility, which intensifies the expression of radius incompletus

In the radius incompletus line N 195, which gives a complete mani-
festation of radius incompletus, in one of the generations, among 36 flies
6 appeared in which the character radius incompletus was expressed in an
extremely strong degree. One of the wings of these flies is represented in
figure 5.

Crosses of these strongly expressed radius incompletus flies with one
another and with usual radius incompletus flies were made, but these
crosses gave no offspring. In further generations of the same line such
flies appeared again but we never succeeded in obtaining progeny from
crosses of these flies between themselves or with any other flies. All
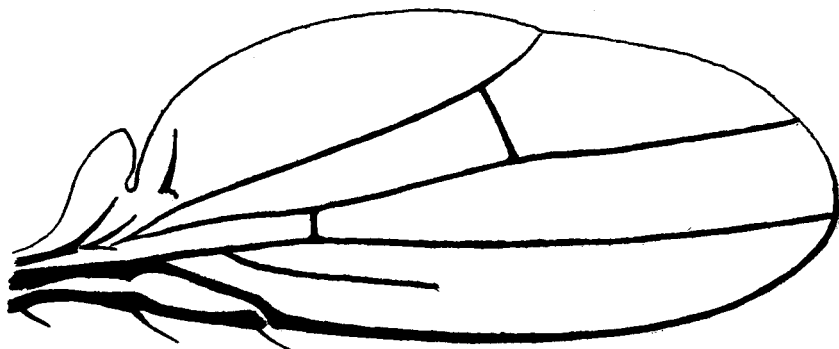
FIGURE 5

these flies proved to be absolutely sterile. The apparition of these sterile
strongly expressed radius incompletus flies in culture N 195 is repre-
sented in diagram 18.

The peculiarities of this apparition are such as to lead to the supposition
that this change depends upon the presence of a recessive gene, which in
homozygous condition provokes sterility and a strong expression of radius
incompletus.

Several of these sterile flies, males and females, were dissected. In the
males no changes in the sexual apparatus were revealed, but the dissec-
tions were unsuccessful, for these males had previously lain a long time in
alcohol. The dissection of females revealed an incomplete development of
ovaries and diminished and deformed receptaculi seminis. The sexual
apparatus of one of these females is represented in figure 6, where, near
the left ovary and the right receptaculum seminis, there are represented
by a dotted line the contours of these organs in a normal fly. A more
detailed anatomic-histological investigation of these flies had not been
carried out.
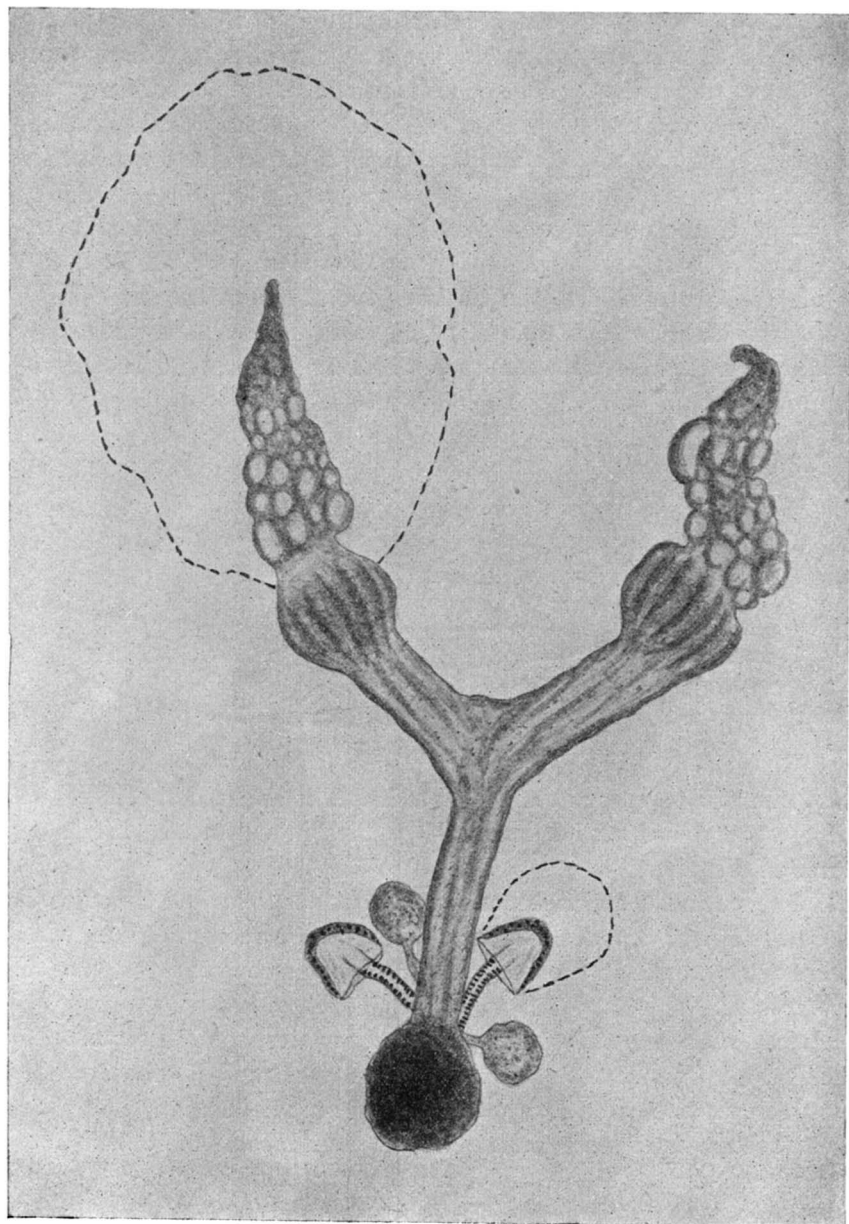
FIGURE 6

d. The effect of the genovariation Alae divergentes on
the expression of radius incompletus

During the work upon the determination of linkage groups, among the genovariations of *Drosophila funebris*, a radius incompletus—Alae divergentes line was obtained. Alae divergentes is a dominant genovariation located in the same chromosome as radius incompletus and lethal in homozygous condition. In flies heterozygous for this gene (the homozygous ones perish) the wings are spread and placed perpendicularly to the body.
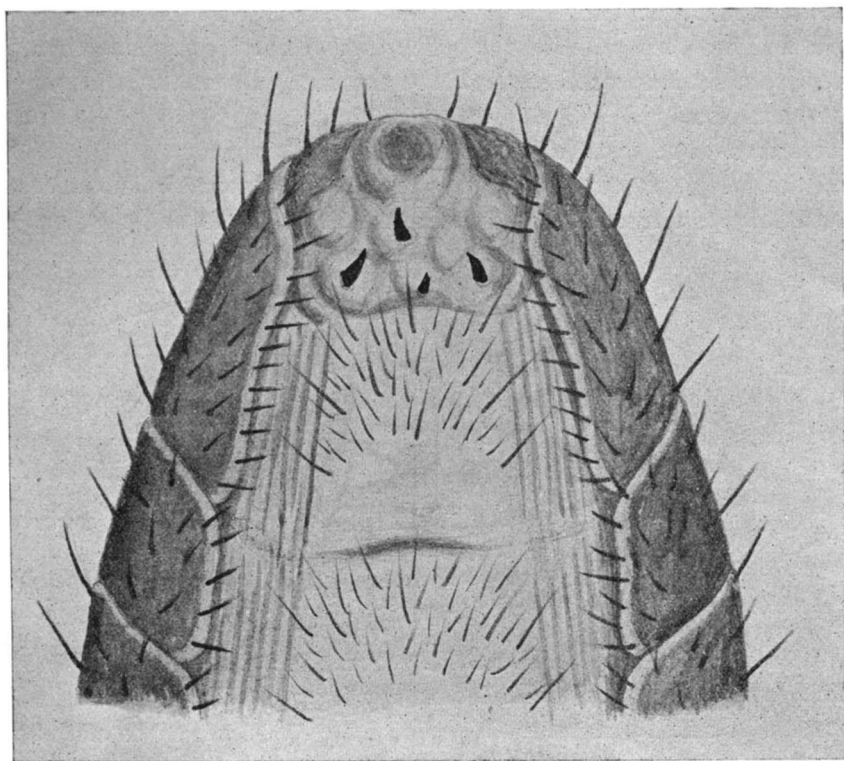
FIGURE 7

Thanks to the recessive lethality of Alae divergentes, the culture, radius incompletus—Alae divergentes, gives in crossing flies which among themselves exhibit the ratio of 2 radius incompletus—Alae divergentes to 1 radius incompletus. In these cultures the radius incompletus character is usually expressed more strongly in those flies which show the character Alae divergentes. Radius incompletus is expressed in radius

incompletus—Alae divergentes flies in the same degree as represented in figure 5.

The effect of Alae divergentes on radius incompletus is not yet completely investigated, for no special attention was paid during this work to variations in the degrees of expression of radius incompletus.

e. The reduction of the genitalia in males connected
with a strong expression of radius incompletus

In one of the generations of the pure normal culture L 5 two males appeared with extremely reduced genitalia. From the same generation of this culture a female was taken for a cross with a radius incompletus male, which bore in addition the venae transversae incompletae character (the incompleteness or absence of the second and sometimes also of the first transverse vein).

This cross is represented in diagram 19.

In the first generation all the flies proved to be normal. In the second generation 86 normal flies and 27 radius incompletus and rad. inc.—v.
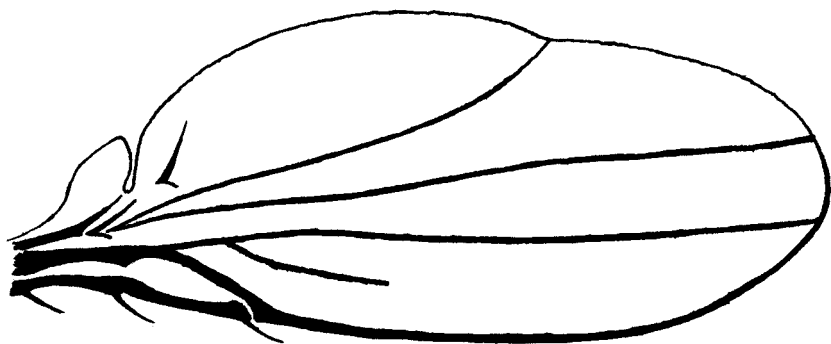
FIGURE 8

transv. inc. flies appeared. From this generation a culture was established which gave only radius incompletus or rad. inc.—v. transv. inc. flies.

As can be seen in diagram 19, three of the five generations of this line each gave several males without genitalia. In all these males, the characters radius incompletus and rad. inc.—v. transv. inc. were strongly expressed. In figure 7 is represented the posterior end of the abdomen of one of these males and in figure 8 his wing. In all these males only a third of the radius remained and the two transverse veins were completely absent.

The peculiarities of the apparition of males without genitalia in this line lead to the inference that this character is a hereditary one, but is hardly connected with only one gene.

f. Venae transversae incompletae

This character is being investigated now, and the results of these investigations will be communicated separately; I will point out only its connection with radius incompletus.

The phenotypic manifestation of this character varies greatly. The different degrees of its expression are represented in drawings 9–12. The
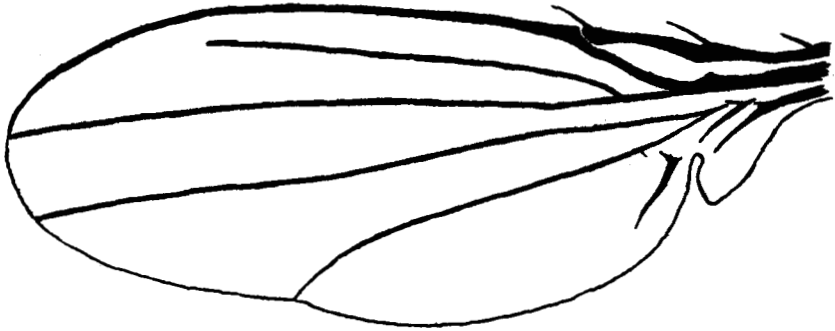
FIGURE 9

degree of phenotypic manifestation and expression of this character depends upon genotypic and external conditions.

The manifestation of this character is possible only in connection with radius incompletus. A fly in which this character manifested itself in the absence of radius incompletus in its genotype was never obtained. Venae
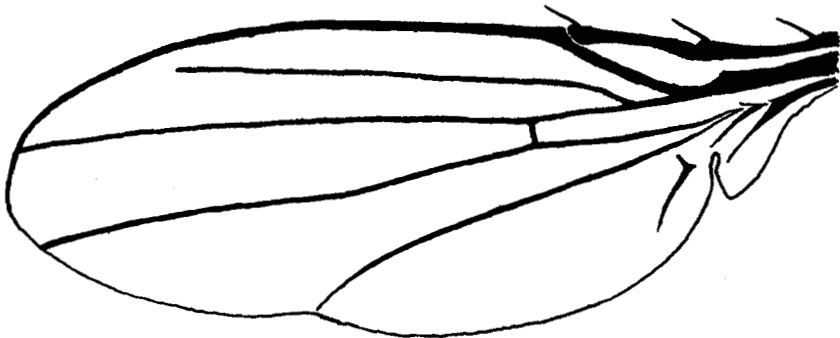
FIGURE 10

transversae incompletae can manifest itself either in a fly homozygous for radius incompletus, or, sometimes, in a heterozygous one, often provoking at the same time the manifestation of radius incompletus in such a heterozygous fly.

Venae transversae incompletae proves to be a hereditary character, the manifestation and expression of which is irregular and depends upon

a series of genotypic and external conditions, but which can be manifested only in the presence of the radius incompletus gene either in the homozygous, or, sometimes, in the heterozygous condition.
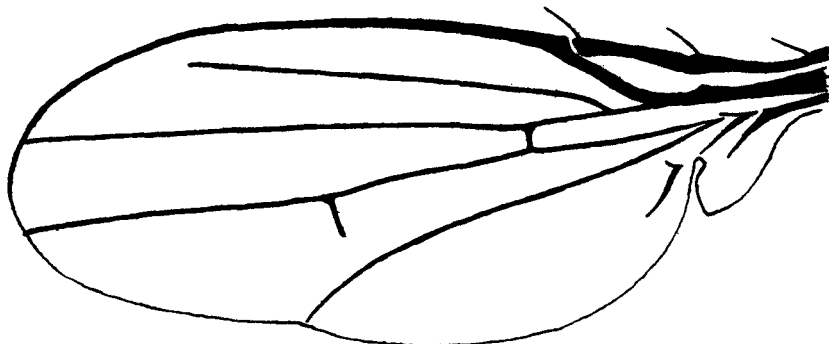
FIGURE 11
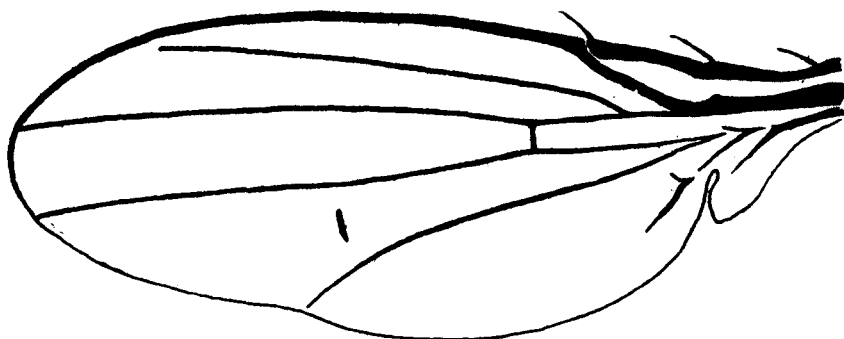
FIGURE 12

THEORETICAL PART

Different "strength" of phenotypic manifestation of radius incompletus in different lines

It is easy to perceive from all the above-mentioned facts, that the radius incompletus character depends upon a recessive gene. The phenotypic manifestation of this gene is in no strong way connected with the effect of certain external conditions which can be controlled during the usual course of cultivation. But in spite of this the radius incompletus character is phenotypically very variable in different lines homozygous for this gene.

In different lines the degree of phenotypic expression of this character varies greatly, from an almost normal structure of the radius to a degree represented in figures 5 and 8. The degree of phenotypic expression

had not been an object of special study during this work, but some cases of strong hereditary variations of the expression of radius incompletus, given above, enable us to suppose that a great hereditary variability of the phenotypic expression of this gene could be obtained with the aid of a more precise accounting.

In all that concerns the degree of phenotypic manifestation and the degree of dominance of radius incompletus we also observe a great variety in different lines.

All the numbers obtained for the 15 different radius incompletus lines mentioned in this work are summarized in table 40. These 15 lines are placed according to the increase of the "strength of manifestation" of radius incompletus. In the first vertical column are given the totals of pure cultures and the percent of the phenotypically normal flies in them. In the second column is given the first generation of the crosses with the pure normal line L 5; in the third column, the second generation of the same crosses. The fourth and the fifth columns give the same generations of crosses with the normal pure line K II.

The general review of all radius incompletus lines obtained reveals the dependence of the phenotypic manifestation and expression of the given gene upon one or another genotype, which includes it. Herewith some circumstances are revealed which it is necessary to note.

As is to be seen in table 40, each radius incompletus line is characterized by a certain "strength of manifestation" of this gene. If we take into consideration all lines we can see that this "strength of manifestation" has for radius incompletus definite limits. Among the 15 lines represented in table 40, the "feeblest" line, "A," gives about 66 percent of radius incompletus manifestation and the "strongest" lines (N 180 and N 81) give fully 100 percent of phenotypic manifestation in a pure culture and about 6 percent of dominance in crosses with normal lines L 5 and K II. All the other lines are placed between these two limits. If we take into consideration some other lines[4] obtained by me, but which are not represented in this table, these limits will be a little enlarged.

Among these lines unrepresented in the table were two lines "feebler" than line "A." In one of these lines, among 542 flies 214 proved to be phenotypically normal, which makes 39.4 percent of non-manifestation of radius incompletus, and the other gave 36 percent of phenotypically normal flies. A line "stronger" than lines N 81 and N 180 was also ob-

[4] During my work I obtained a series of lines, which I have not described here, because I did not want to encumber this article with superfluous material, for they offered no new facts, and also sometimes because sufficient numbers of flies were not obtained.

tained; in the first generation of the cross between this line and the normal line L 5, among 197 flies obtained 34 proved to be radius incompletus, which makes about 17 percent of dominance. Thus taking as a basis all the materials I had, I must consider as limits for the "strength of manifestation" of radius incompletus, on the one hand, 40 percent of non-manifestation, and on the other hand, 15 percent of dominance. It is possible that these limits may be still further apart, though in the formation of my lines flies of several quite different populations took part.

The radius incompletus gene manifests itself in various genotypes in a different degree. The abundance of different radius incompletus lines obtained, the results of crosses between these lines, the experiments made with selection in heterogeneous lines that were homozygous for radius incompletus, and also the mode of origination of the radius incompletus lines, reveal the fact that the genotypic differences between these lines are in most cases polyhybridous. The effect of single genes on the manifestation of radius incompletus is evidently in most cases not very specific, which fact is revealed not only by the polyhybridity, but also by the results of crosses between a given radius incompletus line and different normal ones, and between a given normal line and different radius incompletus lines. Only in comparatively rare cases did we have to deal with definite separate genes, "intensifiers" or "inhibitors".

Data presented in this work prove the multiple effect of a gene. If a definite character depends not only upon the fundamental gene, but also upon the genotype in which this fundamental gene is included, then necessarily the reverse confirmation of the multiple effect of genes arises.[5]

It must also be noted that the strength of phenotypic manifestation of radius incompletus can be quite independent of the strength of its expression. Among the lines obtained by me there are some "feeble" in the degree of manifestation of radius incompletus, which at the same time give a strong degree of expression of this character (for instance lines N 173 and "C"). Among lines which are strong in the degree of manifestation are some also strong in the degree of expression of radius incompletus (line N 81 and two lines which are not represented in table 40), but there are also some feeble in the latter respect (namely, lines N 116 and N 180). The question concerning the independence of the strength of phenotypic manifestation and of the strength of phenotypic expression of the character is of great interest but it requires further investigations.

[5] PLATE, V. HAECKER and others use in such cases the term "pleiotropic" genes.

The recessiveness and dominance of radius incompletus

In some radius incompletus lines we observed the transition of this character to a partially dominant condition.

When a radius incompletus fly is crossed with a normal one, then the genotypes of the parents, considered separately, will be unimportant for the manifestation of radius incompletus in the first generation; the important genotype will be the genotype of the flies of the first generation, which arises as a result of the mixture of the two original genotypes.

It is to be seen in table 40 that lines were obtained which dominated in crosses with the normal line L 5 as well as with the normal line K II. But there are also radius incompletus lines which dominate only in crosses with a given one of these normal lines. One of the lines in table 40 (line "D") gives constantly a certain percent of phenotypically normal flies, but, in spite of this, it dominates in crosses with the normal line K II. In line "D" the genotype is not so favorable for radius incompletus as to give fully 100 percent of manifestation of this character. No genes which behaved as absolute dominant intensifiers of radius incompletus are to be found in the line K II either; this is evident because in the crosses of this normal line with a series of radius incompletus lines, it revealed no dominance. But, evidently, the combination of a series of genes of line "D" with a series of genes of line K II does create a genotype favorable for the manifestation of radius incompletus.

In most cases a specific "intensifying" or "inhibiting" effect on the manifestation of radius incompletus is produced by definite genotypes, that is, combinations of genes, and not by single genes.

Dominance or recessiveness are no specific properties of the radius incompletus gene itself; they too depend upon what genotypic ground this gene will fall on. The one or the other genotype makes the given gene either recessive or dominant.

Sex-limitation of radius incompletus

It has already been mentioned in the beginning of this work that the manifestation of radius incompletus is partly sex-limited. In "feeble" lines the majority of phenotypically normal flies proved to be females. When a great number of lines had been obtained, it was found that the same observation had been made in all "feeble" lines.

The percent of phenotypically normal females and males was calculated for eight "feeble" lines. The general percent of phenotypically normal flies is different in different lines and therefore it is difficult to compare the percents of phenotypically normal females and males in different

lines. In order to avoid this difficulty and to obtain comparable numbers for all lines I calculated for each line the index of sex-limitation. This index represents the proportion between the percent of phenotypically normal females and the percent of phenotypically normal males in the given line.

In table 41 all numbers concerning the sex-limitation in eight "feeble" radius incompletus lines are represented, placed according to the increase of the "strength" of manifestation of radius incompletus. The indices of sex-limitation in these lines are given in the last column. As can be seen in table 41 the index of sex-limitation is different in different lines, but a curious rule was observed concerning this index: the "stronger" the line, the greater is the index of sex-limitation. It is difficult to give a satisfactory explanation for this fact without a special detailed investigation of it. But, in any case, the lawfulness in the variations of the index of sex-limitation, which are always directly proportional to the variations of the strength of manifestation of radius incompletus in different lines, confirms the opinion, that the sex-limitation depends upon a condition not unconnected directly with the genotypic differences between these eight lines.

The reason for this lawfulness can be explained in the following way. Evidently females have a condition which makes the phenotypic manifestation of radius incompletus difficult, and which is permanent in all lines. Many other factors, or conditions, which embarrass the phenotypic manifestation of radius incompletus are to be found in males and females of the "feeble" lines, and among them this sex-limited condition of the female is of no great importance. The index of sex-limitation is therefore small in "feeble" lines. The sex-limiting condition of the female which embarrasses the phenotypic manifestation of radius incompletus is in "strong" lines almost the only unfavorable cause for the manifestation of radius incompletus, and the index of sex-limitation is therefore greater in "stronger" lines.

The above stated concept can of course be used only as a basis for further study of the partial sex-limitedness of the hereditary factors in Drosophila. To explain the latter phenomenon it is necessary to study a series of partially sex-limited hereditary characters, and only after this it will be possible to try to connect this phenomenon with the general concepts existing nowadays concerning the determination of sex and of secondary sex-characters in insects.

The full characterization of the 15 radius incompletus lines described is to be seen in table 42. The degree of manifestation in a pure culture,

given in percents of phenotypic manifestation, the results of crosses with normal lines L 5 and K II, the index of sex-limitation and the degree of phenotypic expression of radius incompletus are given there. The degree of phenotypic expression of radius incompletus is determined by inspection and divided into three categories: strong, average, feeble.

The phenotypic manifestation of the genotype

A definite notion, though still a general and abstract one, of the character of the connection between the genotype and phenotype, is created by the study of the phenotypic manifestation and expression of hereditary characters. This connection is undoubtedly not so simple as it appeared at first, after the first Mendelian work, when one was inclined to find a direct connection between a definite gene and a definite character, and supposed the organism to be integrated of different characters.

Taking into consideration the dependence of the phenotypic manifestation and expression of the gene upon the genotype in which it is included, and the notion, connected with it, of the multiple effect of genes and their reciprocal effects in development, we come to the following notions of the reciprocal relations between the genotype and the pheno-type.

In its manifestation and development the genotype acts as a complete, unique system. The dependence of the phenotype upon the genotype must be a very complicated one, for we must not forget that, though the individual embryological development proves to be like a sum of definite hereditary factors, the function of one genotype, it represents a definite system, involving a mechanism and a definite dependence of some parts of it upon others. And, of course, like every natural phenomenon, the mechanism of individual development has its definite variability which can be connected with the direct effect of definite external conditions and may depend upon more complicated causes. This variability must be of great importance in the realization of different small peculiarities and characters, hereditary as well as non-hereditary, in the phenotype of an adult specimen. Taking all this into consideration we are enabled to create for ourselves a notion of the causes of incomplete and irregular manifestation of some hereditary characters and of radius incompletus in particular.

If one takes a series of pure "feeble" radius incompletus lines one finds a non-manifestation of this character in a definite proportion of specimens, and this non-manifestation is a purely phenotypic one, for it allows no selection within the limits of each given pure line. No direct

(sufficiently strong) effect of definite external conditions is to be observed. In each given line the character attains phenotypic manifestation in a definite percent of cases, and this percent is different in many lines. This can be compared to a man who shoots at a target and has guns of different qualities—if the gun is good he will hit the target in a greater percent of cases; if the gun is bad, in a smaller. I imagine the manifestation of radius incompletus as follows. The genotype in "feeble" lines is of such a character that it can not produce the manifestation of radius incompletus under all conditions. Different genotypes are favorable to the manifestation of this character to a different degree, as if they each give an impulse of different strength for the manifestation of it. The mechanism of individual development varies. This variation gives, of course, a very complicated system of variability; some variations of this system may be less favorable to the manifestation of radius incompletus than others. If one represents, conditionally, this variation of individual development as a normal curve, then one can consider that a definite genotype produces the phenotypic manifestation of the radius incompletus character only in the variants in a definite part of the area of this curve, and that different genotypes can occupy, in respect to the manifestation of radius incompletus, different parts of this area. The illustration of this supposition is given in diagram 20. One line can give the manifestation of the character in specimens placed between the 1st and 9th marked ordinates of the curve, another line gives this manifestation in specimens placed between the 4th and 11th ordinates, and so on. The "strongest" lines give the manifestation of the character in all cases independently of variations in the system of individual development. One could verify the reality of the ideas above stated by experiments, producing changes in the mechanism of individual development and observing the effect of these changes on the phenotypic manifestation of radius incompletus.

All the above stated facts lead us also to the comprehension of the hereditary constitution. The significance of the hereditary constitution may consist of: (1) a purely genetic dependence of genes upon one another in their manifestation, and in connection with this the hereditary predisposition of hereditary characters to a definite form of phenotypic manifestation; (2) the formation of hereditary predispositions to external effects (diseases, effect of temperature, poisons and so on); (3) the fact, that in a definite hereditary constitution there may be present a hereditary character (or characters), which can affect the manifestation of a series of hereditary and non-hereditary characters not as a gene but purely phenotypically as a character.

It can be seen from the above presented material that each genotype, that differs by something from others, represents a kind of hereditary constitution, which differs only conditionally from what we practically consider as being such.

Some cases of applying the above-mentioned point of view concerning the phenotypic manifestation of the genotype

We are able to give a satisfactory characterization to a series of cases met with in genetic investigations from the point of view mentioned in the preceding paragraph. First of all a series of cases of irregular inheritance. Some genes are so little specific[6] that they manifest themselves in a small percent of cases and, in connection with this, give Mendelian ratios which deviate extremely from the expected ones.

The hereditary tumors in *Drosophila melanogaster*, as well as one of the genovariations in *Drosophila funebris* which is expressed, in cases of phenotypic manifestation, by the formation of sprouts on the second transverse vein of the wing,[7] can serve as extreme examples of this kind. Several other genes (abnormal abdomen, bifid, club, balloon, streak, dumpy, truncate, vortex, beaded, bent, eyeless and others) form a series of transitions from little specific genes to highly specific genes, which give the phenotypic manifestation under all conditions.

It is curious to note that the high specificity of a gene is not always connected with its dominance. There are little specific recessive genes (as hereditary tumors in *Drosophila melanogaster*, club, vortex, eyeless and radius incompletus), completely specific recessive genes (white, black, spineless and others), little specific dominant genes (abnormal abdomen, beaded, truncate) and completely specific dominant genes (bar in *Drosophila melanogaster* and Alae divergentes in *Drosophila funebris*).

The small specificity of the gene provokes a small resistance to external and internal influences in its manifestation. The phenotypic manifestation and expression of these genes vary usually in a high degree and some of the genes prove to be, in their phenotypic manifestation, subject to the influence of definite external conditions (abnormal abdomen), others are subject to genotypical influences (radius incompletus), and some others to both of these influences (beaded).

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[6] I consider as a specific gene, a gene which is able to give a definite degree and form of phenotypic manifestation and expression in spite of different influences. The less specific is the gene, the more changeable is the degree and form of its phenotypic manifestation and expression.

[7] This genovariation served as material for a work of E. A. TIMOFÉEFF-RESSOVSKY which is not yet published.

It is quite possible that some cases of the asymmetrical manifestation of hereditary characters can be explained from the point of view, that the phenotypic manifestation of little specific genes depends upon variations of the individual development. In the process of individual development, especially in the latest more differentiated stages, the placement of organs on the one and the other sides can evidently vary independently one of another and thus provoke an asymmetry in the phenotypic manifestation of the little specific gene.

If one takes into consideration the effect of a genotype on the phenotypic manifestation of a separate gene, one can explain some cases where an effect of selection on a Mendelian ratio takes place. It seems to me that the positive results obtained in the work of LITTLE and JONES with the genovariation eyeless in *Drosophila melanogaster* can be explained by the facts, that the genotype which gives the largest percent of phenotypic manifestation has been selected on the one hand, and on the other the genotype which gives the least percent of phenotypic manifestation of this gene.

CONCLUSION

The study of the conditions under which different hereditary characters manifest themselves phenotypically would be of great importance in the explanation of the fundamental phenomena of heredity. The absence of this material nowadays prevents us from connecting Mendelism with the mechanics and physiology of development, and without this we are not able to construct a real notion of the nature of the gene and its effects in the manifestation of hereditary characters. The study of the conditions for the phenotypic manifestation of hereditary characters must be the fundamental problem of phenogenetics, some ways of investigation of which were indicated by HAECKER.

SUMMARY

1. The recessive autosomal genovariation radius incompletus has been described; the study of this genovariation revealed that it gave in a series of lines an incomplete phenotypic manifestation.

2. The study of the percent of phenotypic manifestation of radius incompletus, in a series of genotypically different lines, revealed that the degree of phenotypic manifestation and expression of radius incompletus depends upon the genotype which includes the fundamental radius incompletus gene.

3. Different radius incompletus lines were obtained, which gave from 60 percent to 100 percent of phenotypic manifestation of this gene.

4. Some radius incompletus lines proved to be incompletely dominant in crosses with certain normal lines.

5. The degree of phenotypic manifestation of radius incompletus and the degree of phenotypic expression of radius incompletus proved to be independent of one another in a series of lines.

6. The phenotypic manifestation of radius incompletus proved to be partially sex-limited. The index of sex-limitation has been calculated, and it was revealed that this index varies in different lines in direct proportion to the degree of phenotypic manifestation of radius incompletus in these lines.

7. The idea of a possible scheme of phenotypic manifestation of the genotype has been expressed, and some cases of application of this scheme have been mentioned.

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TABLE 1

LINE NUMBER 14

Number of crosses	Radius incompletus	Normal	Total
1	226	26	252
2	171	19	190
3	279	33	312
4	188	20	208
5	209	23	232
Totals	1073	121	1194
Percent normals	10.13 ± 0.80		

TABLE 2

LINE NUMBER 16

Number of crosses	Radius incompletus	Normal	Total
1	211	24	235
2	189	20	209
3	228	27	255
4	264	31	295
5	236	29	265
Totals	1128	131	1259
Percent normals	10.41 ± 0.80		

TABLE 3

LINE NUMBER 13

Number of crosses	Radius incompletus	Normal	Total
1	217	..	217
2	279	2	281
3	227	..	227
4	193	..	193
5	236	1	237
Totals	1152	3	1155
Percent normals	—————— " ——————		

TABLE 4

OFFSPRING OF RADIUS INCOMPLETUS PARENTS FROM HOMOZYGOUS RADIUS INCOMPLETUS LINES				OFFSPRING OF PHENOTYPICALLY NORMAL PARENTS FROM THE SAME LINES			
	Radius incompletus	Normal	Total		Radius incompletus	Normal	Total
Line number 14	199	24	223	Line number 14	311	36	347
	288	32	320		201	25	226
	192	22	214		219	25	244
Totals	679	78	757	Totals	731	86	817
Percent normals	10.30 ± 1.06			Percent normals	10.52 ± 0.98		
Line number 16	212	25	237	Line number 16	259	29	288
	261	31	292		296	38	334
	328	39	367		272	31	303
Totals	801	95	896	Totals	827	98	925
Percent normals	10.60 ± 0.97			Percent normals	10.53 ± 0.96		

TABLE 5

NUMBER OF LINES	TOTAL COUNTS OF FLIES				RADIUS INCOMPLETUS		PHENOTYPICALLY NORMAL FLIES		PERCENT OF PHENOTYPICALLY NORMAL FLIES IN THE SEXES	
	Total	♀♀	♂♂	Sex ratio	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
Number 14	780	388	392	1 :1 .01	323	372	64	17	16.49	4.34
Number 16	699	344	355	1 :1 .03	288	340	56	15	16.28	4.22

TABLE 6

F$_2$ FROM CROSSES.
RADIUS INCOMPLETUS NUMBER 14×NORMAL L5

Number of crosses	Normal	Radius incompletus	Total
1	142	44	186
2	204	63	267
3	227	71	298
4	183	56	239
5	196	59	255
Totals	952	293	1245
F$_2$ ratio.	3.24 ± 0.16 :1		

TABLE 7

F$_2$ FROM CROSSES.
RADIUS INCOMPLETUS NUMBER 16×NORMAL L5

Number of crosses	Normal	Radius incompletus	Total
1	157	44	201
2	293	89	382
3	210	61	271
4	152	46	198
5	161	47	208
6	228	64	292
Totals	1201	351	1552
F$_2$ ratio.	3.42 ± 0.19 :1		

TABLE 8

F$_2$ FROM CROSSES.
RADIUS INCOMPLETUS NUMBER 13×NORMAL L5

Number of crosses	Normal	Radius incompletus	Total
1	232	78	310
2	173	56	229
3	211	69	280
4	197	64	261
5	208	68	276
6	265	89	354
Totals	1286	424	1710
F$_2$ ratio.	3.03 ± 0.15 :1		

TABLE 9

F$_2$ FROM CROSSES.
RADIUS INCOMPLETUS NUMBER 14×NORMAL KII

Number of crosses	Normal	Radius incompletus	Total
1	144	38	182
2	200	53	253
3	221	61	282
4	151	41	192
5	297	84	381
Totals	1013	277	1290
F$_2$ ratio.	3.66 ± 0.21 :1		

TABLE 10

F₂ FROM CROSSES.
RADIUS INCOMPLETUS NUMBER 16×NORMAL K II

Number of crosses	Normal	Radius incompletus	Total
1	194	53	247
2	263	70	333
3	231	61	292
4	181	49	230
5	251	65	316
Totals	1120	298	1418
F₂ ratio.	3.76 ± 0.21 :1		

TABLE 11

F₂ FROM CROSSES.
RADIUS INCOMPLETUS NUMBER 13×NORMAL K II

Number of crosses	Normal	Radius incompletus	Total
1	183	54	237
2	231	69	300
3	203	62	265
4	162	49	211
5	227	67	294
6	254	77	331
Totals	1260	378	1638
F₂ ratio.	3.33 ± 0.20 :1		

TABLE 12

LINE NUMBER 173

Number of crosses	Radius incompletus	Normal	Total
1	257	43	300
2	182	32	214
3	171	33	204
4	286	50	336
5	104	17	121
6	130	24	154
7	173	29	202
Totals	1303	228	1531
Percent normals	14.89 ± 0.85		

TABLE 13

F₂ FROM CROSSES.
RADIUS INCOMPLETUS NUMBER 173×RADIUS INCOMPLETUS NUMBER 13

Number of crosses	Radius incompletus	Normal	Total
1	126	5	131
2	103	4	107
3	109	5	114
4	119	5	124
5	141	6	147
Totals	598	25	623
Percent normals	4.01 ± 0.80		

TABLE 14

F₂ FROM CROSSES.
RADIUS INCOMPLETUS NUMBER 173×NORMAL K II

Number of crosses	Normal	Radius incompletus	Total
1	127	35	162
2	176	48	224
3	88	27	115
4	141	41	182
Totals	532	151	683
F_2 ratio.		3.52 ± 0.27 :1	

TABLE 15

LINE NUMBER 81

Number of crosses	Radius incompletus	Normal	Total
1	183	..	183
2	213	..	213
3	154	..	154
4	227	1	228
5	142	..	142
6	258	..	258
Totals	1177	1	1178
Percent normals		''	

TABLE 16

F₁ FROM CROSSES.
RADIUS INCOMPLETUS NUMBER 81×NORMAL L5

Number of crosses	Normal	Radius incompletus	Total
1	163	11	174
2	169	11	180
3	97	6	103
4	131	8	139
5	142	9	151
Totals	702	45	747
Percent radius in-completus		6.02 ± 0.80	

TABLE 17

F₂ FROM CROSSING *inter se*
RADIUS INCOMPLETUS FLIES OF TABLE 16

Number of crosses	Normal	Radius incompletus	Total
1	192	65	257
2	183	63	246
3	171	56	227
4	173	59	232
Totals	719	243	962
F_2 ratio.		2.96 ± 0.20 :1	

TABLE 18

F₂ FROM CROSSING *inter se*
NORMAL FLIES OF TABLE 16

Number of crosses	Normal	Radius incompletus	Total
1	122	43	165
2	181	64	245
3	191	61	252
4	178	61	239
5	118	42	160
6	129	43	172
Totals	919	314	1233
F₂ ratio.		2.92 ± 0.19 :1	

TABLE 19

F₁ FROM CROSSES OF RADIUS INCOMPLETUS
NUMBER 81×NORMAL FROM MASS-CULT K II

Number of crosses	Normal	Radius incompletus	Total
1	161	9	170
2	147	8	155
3	128	6	134
4	163	10	173
5	135	7	142
Totals	734	40	774
Percent radius incompletus		5.17 ± 0.77	

TABLE 20

F₂ FROM CROSSING *inter se*
RADIUS INCOMPLETUS FLIES OF TABLE 19

Number of crosses	Normal	Radius incompletus	Total
1	137	47	184
2	79	26	105
3	128	44	172
4	94	32	126
5	131	43	174
Totals	569	192	761
F₂ ratio.		2.97 ± 0.24 :1	

TABLE 21

F₂ FROM CROSSING *inter se*
NORMAL FLIES OF TABLE 19

Number of crosses	Normal	Radius incompletus	Total
1	182	52	234
2	319	103	422
3	174	56	230
4	179	51	230
5	268	75	343
Totals	1122	337	1459
F₂ ratio.		3.33 ± 0.21 :1	

TABLE 22

LINE NUMBER 180

Number of crosses	Radius incompletus	Normal	Total
1	213	..	213
2	292	..	292
3	184	1	185
4	232	..	232
5	281	..	281
Totals	1202	1	1203
Percent normals		——————— ″ ———————	

TABLE 23

F₁ FROM CROSSES.
RADIUS INCOMPLETUS NUMBER 180×NORMAL L 5

Number of crosses	Normal	Radius incompletus	Total
1	126	7	133
2	108	6	114
3	76	4	80
4	93	5	98
Totals	403	22	425
Percent radius in- completus		5.18 ± 0.92	

TABLE 24

F₂ FROM CROSSING *inter se*
RADIUS INCOMPLETUS FLIES OF TABLE 23

Number of crosses	Normal	Radius incompletus	Total
1	181	56	237
2	119	42	161
3	176	57	233
4	189	62	251
5	165	54	219
Totals	830	271	1101
F₂ ratio.		$3.06 \pm 0.21 : 1$	

TABLE 25

F₂ FROM CROSSING *inter se*
NORMAL FLIES FROM TABLE 23

Number of crosses	Normal	Radius incompletus	Total
1	170	55	225
2	149	51	200
3	123	42	165
4	175	54	229
5	109	34	143
6	163	56	219
Totals	889	292	1181
F₂ ratio.		$3.04 \pm 0.20 : 1$	

TABLE 26

F₁ FROM CROSSES.
RADIUS INCOMPLETUS NUMBER 180×NORMAL K II

Number of crosses	Normal	Radius incompletus	Total
1	158	14	172
2	94	7	101
3	82	5	87
4	117	8	125
5	97	7	104
Totals	548	41	589
Percent radius in-completus	6.96±0.85		

TABLE 27

F₂ FROM CROSSING *inter se*
RADIUS INCOMPLETUS FLIES OF TABLE 26

Number of crosses	Normal	Radius incompletus	Total
1	151	48	199
2	158	52	210
3	165	48	213
4	138	40	178
Totals	612	188	800
F₂ ratio.	3.26±0.25 :1		

TABLE 28

F₂ FROM CROSSING *inter se*
NORMAL FLIES OF TABLE 26

Number of crosses	Normal	Radius incompletus	Total
1	181	55	236
2	122	37	159
3	107	33	140
4	143	46	189
5	133	43	176
6	192	56	248
Totals	878	270	1148
F₂ ratio.	3.25±0.21 :1		

TABLE 29

LINE NUMBER 192	OFFSPRING OF RADIUS INCOMPLETUS PARENTS			LINE NUMBER 192	OFFSPRING OF PHENOTYPICALLY NORMAL PARENTS		
Number of crosses	Radius incompletus	Normal	Total	Number of crosses	Radius incompletus	Normal	Total
1	211	42	253	1	160	32	192
2	116	23	139	2	186	36	222
3	155	32	187	3	268	53	321
4	173	34	207	4	124	23	147
5	205	39	244	5	141	27	168
Totals	860	170	1030	Totals	879	171	1050
Percent normals	16.50 ± 1.17			Percent normals	16.28 ± 1.14		

TABLE 30

F₂ FROM CROSSES.
RADIUS INCOMPLETUS NUMBER 192×NORMAL K II

Number of crosses	Normal	Radius incompletus	Total
1	242	65	307
2	257	67	324
3	132	34	166
4	163	43	206
5	221	57	278
6	124	32	156
Totals	1139	298	1437
F₂ ratio.	$3.82 \pm 0.22 : 1$		

TABLE 31

LINE NUMBER 205

Number of crosses	Radius incompletus	Normal	Total
1	175	..	175
2	186	..	186
3	217	..	217
4	231	..	231
5	158	2	160
6	223	..	223
Totals	1190	2	1192
Percent normals	''		

TABLE 32

F₁ FROM CROSSES.
RADIUS INCOMPLETUS NUMBER 205×NORMAL L 5

Number of crosses	Normal	Radius incompletus	Total
1	156	7	163
2	169	8	177
3	171	8	179
4	158	7	165
Totals	654	30	684
Percent radius in-completus		4.38±0.73	

TABLE 33

F₁ FROM CROSSING *inter se*
RADIUS INCOMPLETUS FLIES OF TABLE 32

Number of crosses	Normal	Radius incompletus	Total
1	176	57	233
2	189	62	251
3	132	43	175
4	160	51	211
5	202	65	267
Totals	859	278	1137
F₂ ratio.		3.09±0.21 :1	

TABLE 34

F₂ FROM CROSSING *inter se*
NORMAL FLIES OF TABLE 32

Number of crosses	Normal	Radius incompletus	Total
1	185	61	246
2	169	53	222
3	213	68	281
4	145	49	194
5	163	55	218
Totals	875	286	1161
F₂ ratio.		3.06±0.20 :1	

TABLE 35

F₁ FROM CROSSES.
RADIUS INCOMPLETUS NUMBER 205×NORMAL K II

Number of crosses	Normal	Radius incompletus	Total
1	148	..	148
2	205	..	205
3	116	1	117
4	128	1	129
Totals	597	2	599
Percent radius in-completus		''	

TABLE 36

Number of crosses	F₁ FROM CROSSING *inter se* NORMAL FLIES OF TABLE 35		
	Normal	Radius incompletus	Total
1	152	47	199
2	184	55	239
3	172	55	227
4	211	68	279
5	193	62	255
Totals	912	287	1199
F₂ ratio.	3.18 ± 0.21 :1		

TABLE 37

LINE NUMBER 163	OFFSPRING OF RADIUS INCOMPLETUS PARENTS			LINE NUMBER 163	OFFSPRING OF PHENOTYPICALLY NORMAL PARENTS		
Number of crosses	Radius incompletus	Normal	Total	Number of crosses	Radius incompletus	Normal	Total
1	220	71	291	1	425	139	564
2	438	143	581	2	194	61	255
3	165	54	219	3	131	42	173
4	194	63	257	4	243	78	321
5	119	38	157	5	166	53	219
Totals	1136	369	1505	Totals	1159	373	1532
Percent normals	24.51 ± 1.05			Percent normals	24.34 ± 1.04		

TABLE 38

F$_2$ FROM CROSSES.
RADIUS INCOMPLETUS NUMBER 163 × RADIUS INCOMPLETUS NUMBER 13

Number of crosses	Radius incompletus	Normal	Total
1	78	..	78
2	69	..	69
3	93	1	94
4	87	1	88
Totals	327	2	329
Percent normals		″	

TABLE 39

F$_2$ FROM CROSSES.
RADIUS INCOMPLETUS NUMBER 163 × RADIUS INCOMPLETUS NUMBER 13

Number of crosses	Radius incompletus	Normal	Total
1	401	25	426
2	109	6	115
3	93	5	98
4	181	11	192
5	147	9	156
Totals	931	56	987
Percent normals	5.67 ± 0.71		

TABLE 40

RADIUS-INCOMPLETUS LINES	IN PURE LINE				F1 FROM CROSSES WITH NORMAL PURE LINE L 5				F2 FROM CROSSES WITH NORMAL PURE LINE L 5				F1 FROM CROSSES WITH NORMAL PURE LINE K II				F2 FROM CROSSES WITH NORMAL PURE LINE K II			
	Total	Radius incompletus	Normal	Percent normals	Total	Normal	Radius incompletus	Percent radius incompletus	Total	Normal	Radius incompletus	F_2 ratio	Total	Normal	Radius incompletus	Percent radius incompletus	Total	Norma	Radius incompletus	F_2 ratio
"A"	2178	1457	721	33.10	307	307	..	..	1068	847	221	3.83:1	293	293	..	..	1099	858	241	3.56:1
"B"	973	787	186	19.12	187	187	..	..	639	494	145	3.42:1	223	223	..	..	620	488	132	3.69:1
No. 192	2080	1739	341	16.39	..	..	..	..	..	..	..	..	314	314	..	..	1437	1139	298	3.82:1
No. 173	1531	1303	228	14.89	..	..	..	..	..	..	..	..	191	191	..	..	683	532	151	3.52:1
No. 16	3080	2756	324	10.52	316	316	..	..	1552	1201	351	3.42:1	271	271	..	..	1418	1120	298	3.76:1
No. 14	2768	2483	285	10.29	253	253	..	..	1245	952	293	3.24:1	248	248	..	..	1290	1013	277	3.66:1
"C"	892	804	88	9.86	172	172	..	..	558	432	126	3.43:1	167	167	..	..	588	451	137	3.29:1
"D"	980	919	61	6.22	217	217	..	..	911	694	217	3.19:1	202	191	11	5.44	844	635	209	3.04:1
No. 13	1155	1152	3	..	421	421	..	..	1710	1286	424	3.03:1	396	396	..	..	1638	1260	378	3.33:1
No. 111	697	697	..	..	341	341	..	..	884	665	219	3.03:1	402	402	..	..	1009	768	241	3.18:1
No. 130	811	811	2	..	372	372	..	..	966	734	232	3.16:1	293	293	..	..	512	385	127	3.03:1
No. 116	798	796	2	..	281	281	..	..	685	518	167	3.04:1	315	302	13	4.12	607	464	143	3.24:1
No. 205	1192	1190	1	..	684	654	30	4.38	2298	1734	564	3.07:1	599	597	2	..	1199	912	287	3.18:1
No. 81	1178	1177	1	..	747	702	45	6.02	2195	1638	557	2.94:1	..	..	..	..	..	..	..	..
No. 180	1203	1202	1	..	425	403	22	5.18	2282	1719	563	3.05:1	598	548	41	6.96	1948	1490	458	3.25:1

TABLE 41

RADIUS INCOMPLETUS LINES	TOTAL COUNTS			RADIUS INCOMPLETUS			PHENOTYPICALLY NORMAL			PERCENTS AND RATIOS				
	Total	♀♀	♂♂	Total	♀♀	♂♂	Total	♀♀	♂♂	Sex ratio	Percent phenotypically normal in the line	Percent phenotypically normal ♀♀	Percent phenotypically normal ♂♂	Index of sex-limitations
"A"	2178	1069	1109	1457	566	891	721	503	218	1:1.04	33.10	47.05	19.65	2.39
"B"	973	477	496	787	338	449	186	139	47	1:1.04	19.12	29.14	9.47	3.07
Number 192	2080	1024	1056	1739	765	974	341	259	82	1:1.03	16.39	25.29	7.76	3.26
Number 173	1531	757	774	1303	581	722	228	176	52	1:1.02	14.89	23.25	6.72	3.46
Number 16	3080	1516	1564	2756	1259	1497	324	257	67	1:1.03	10.52	16.95	4.28	3.96
Number 14	2768	1363	1405	2483	1137	1346	285	226	59	1:1.03	10.29	16.59	4.19	3.95
"C"	892	439	453	804	369	435	88	70	18	1:1.03	9.86	15.95	3.97	4.02
"D"	980	482	498	919	431	488	61	51	10	1:1.03	6.22	10.37	2.01	5.15

TABLE 42

RADIUS INCOMPLETUS LINES	DEGREE OF PHENOTIPIC MANIF. IN PURE LINE	CROSSES WITH L 5		CROSSES WITH K II		INDEX OF SEX-LIMITA-TION	DEGREE OF PHENOTYPIC EXPRESSION OF RADIUS INCOMPLETUS
		F_1	F_2	F_1	F_2		
"A"	66.90%		3.8:1		3.6:1	2.4	medium
"B"	80.88%		3.4:1		3.7:1	3.0	medium
Number 192	83.61%		.....		3.8:1	3.3	slight
Number 173	85.11%		.....		3.5:1	3.5	strong
Number 16	89.48%		3.4:1		3.8:1	3.9	slight
Number 14	89.71%		3.2:1		3.7:1	3.9	medium
"C"	90.14%		3.4:1		3.3:1	4.0	strong
"D"	93.78%		3.2:1	5.44% r. i.	3.0:1	5.2	medium
Number 13	100%		3.0:1		3.3:1		medium
Number 111	100%		3.0:1		3.2:1		strong
Number 130	100%		3.2:1		3.0:1		medium
Number 116	100%		3.0:1	4.12% r. i.	3.2:1		slight
Number 205	100%	4.38% r. i.	3.1:1		3 2:1		medium
Number 81	100%	6.02% r. i.	2.9:1	5.02% r. i.	3.1:1		strong
Number 180	100%	5.18% r. i.	3.1:1	6.96% r. i.	3.3:1		slight

DIAGRAM 1

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DIAGRAM 2

DIAGRAM 3

r.i. *16   ♂ r.i. *14. a.div.   ♂ r.i. *178

83   2   19 div.   22 norm

*180

a.div.18   21

66   3

72   3   42   4

77   2   68   5

117   3   92   13

94   126   18

223   164   23

441   163   25   172   24
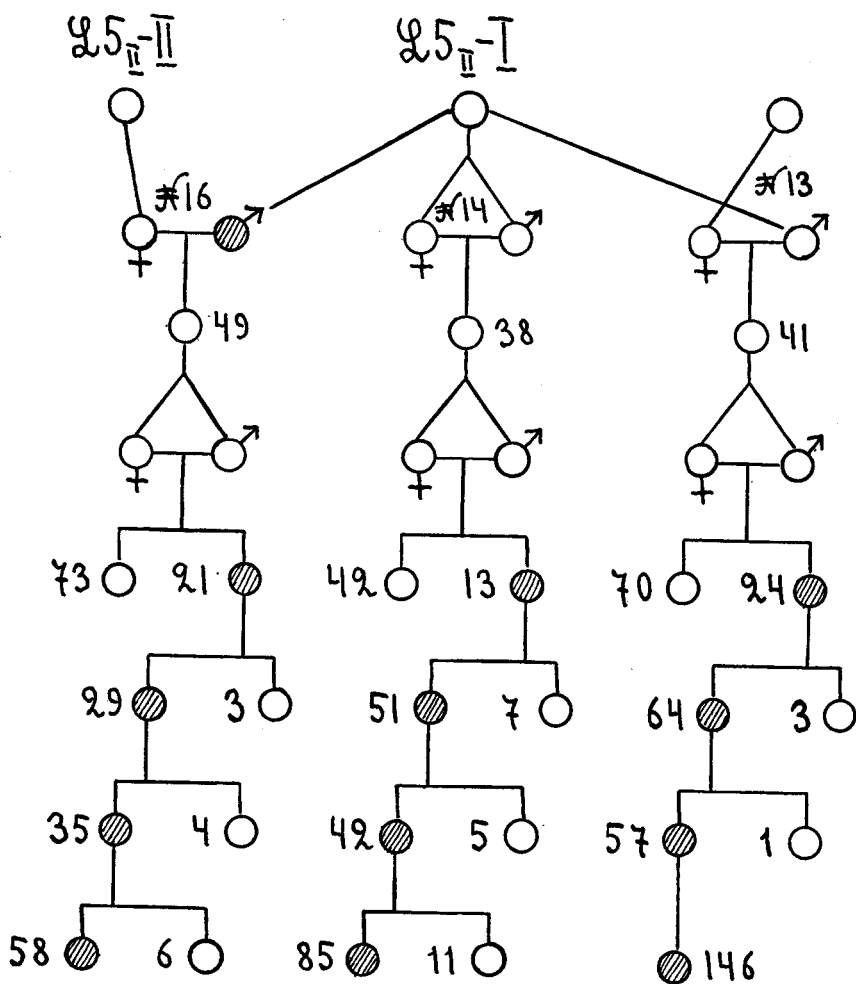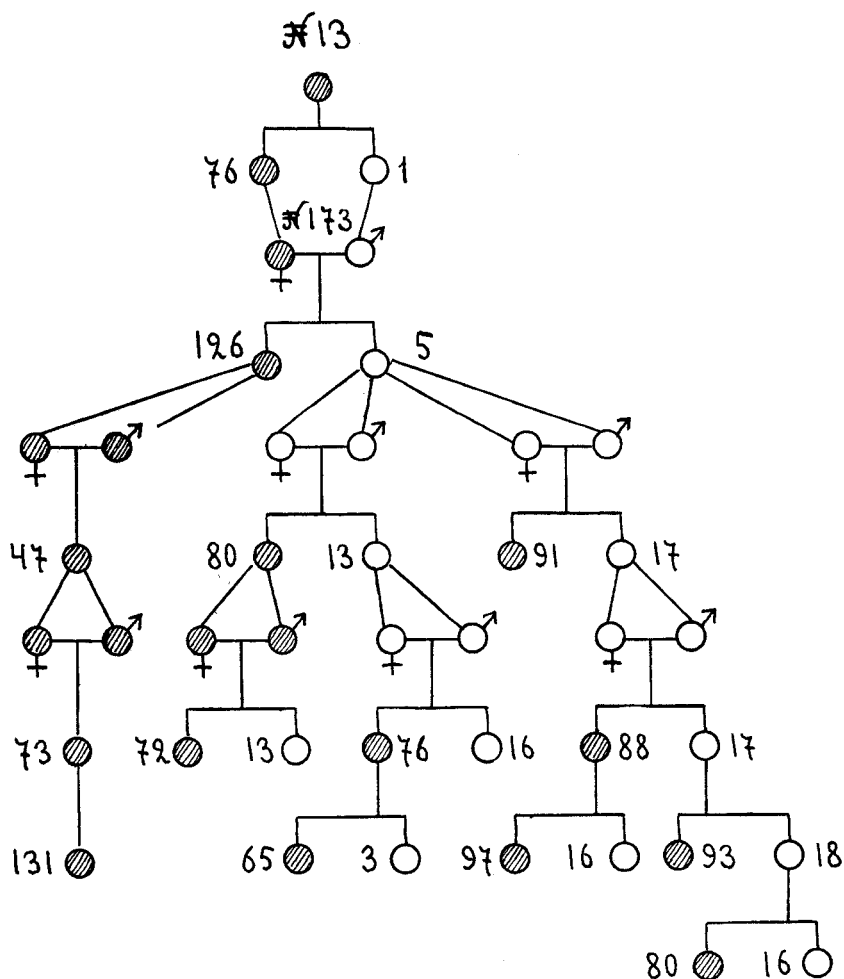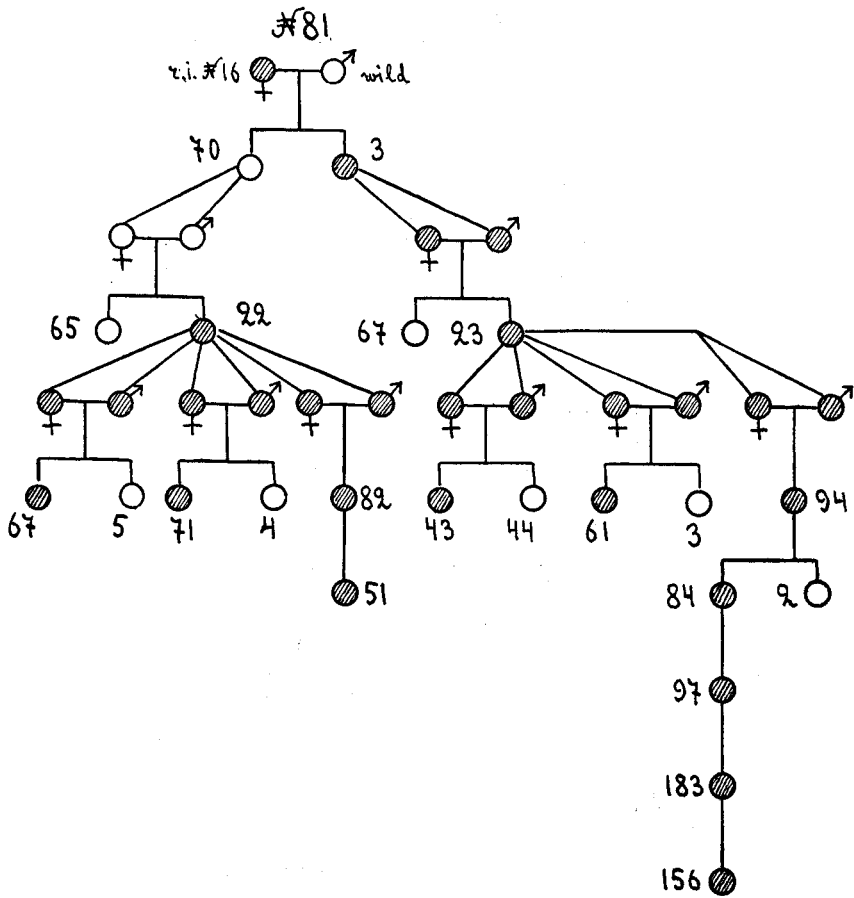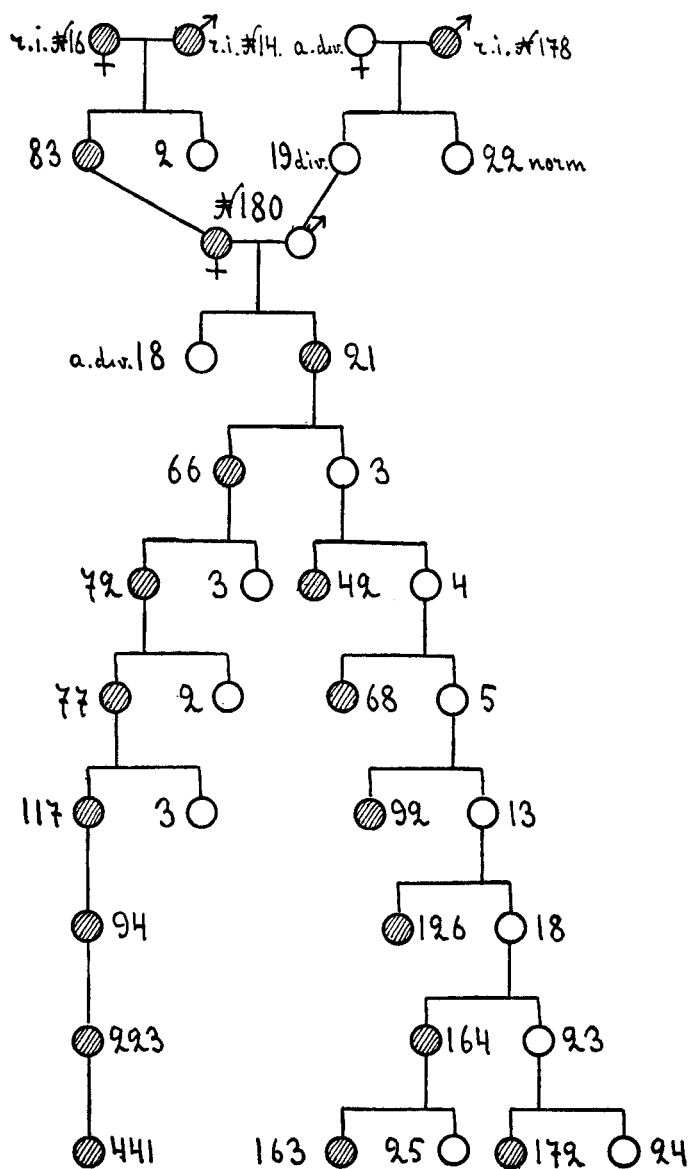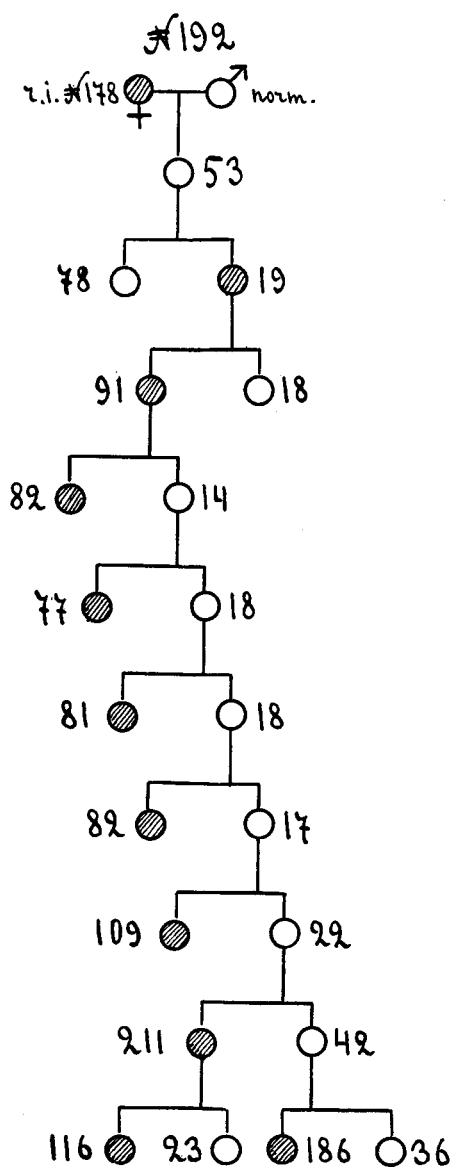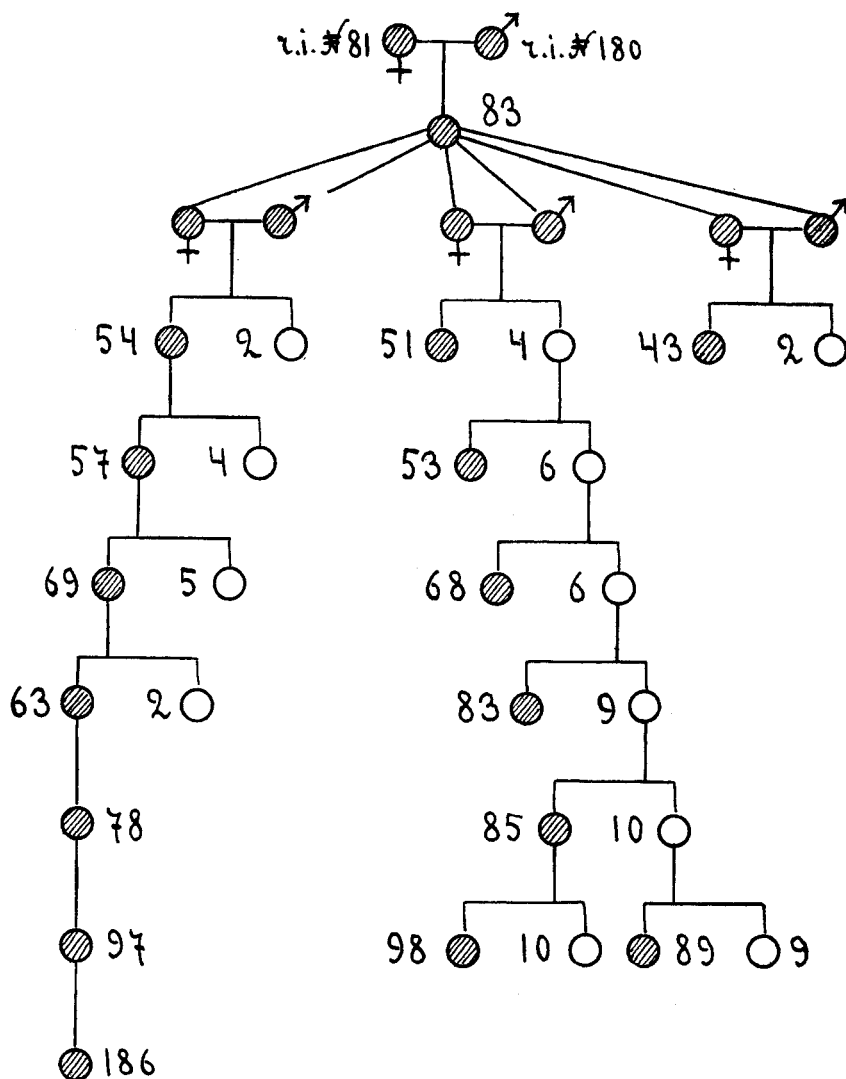
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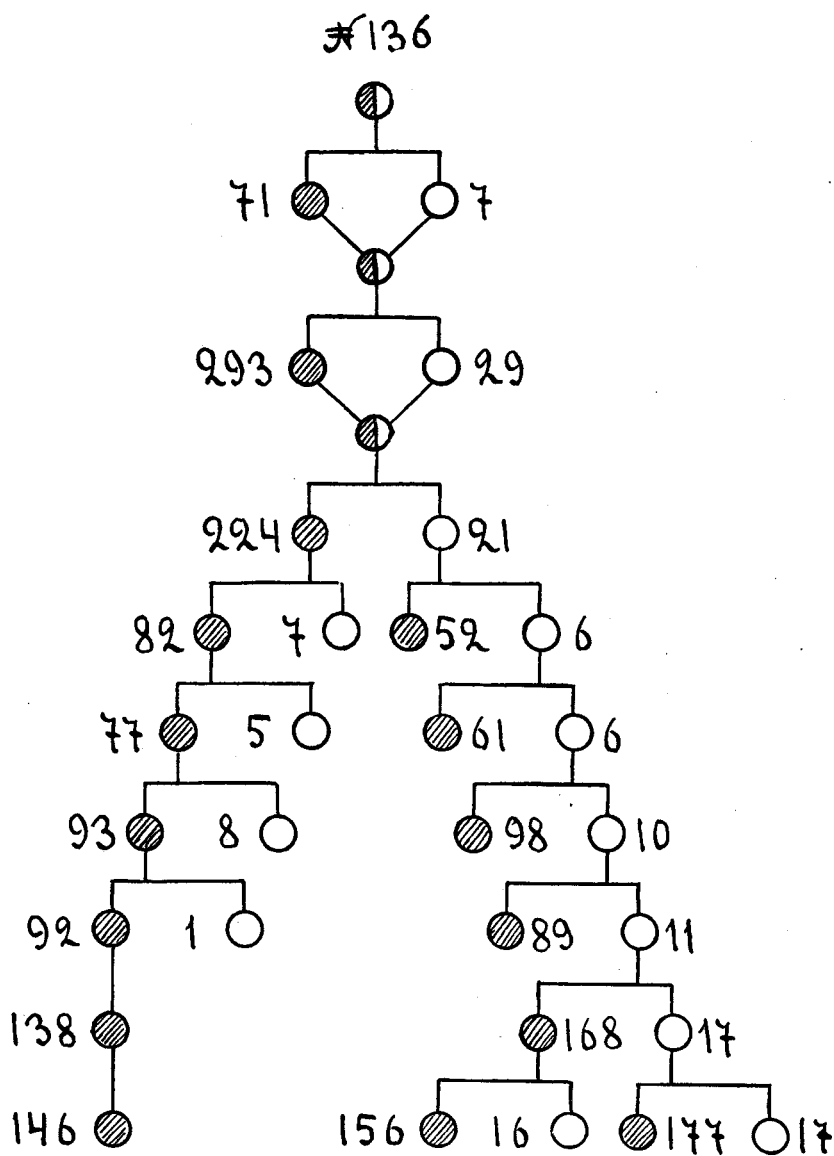
DIAGRAM 5

DIAGRAM 6
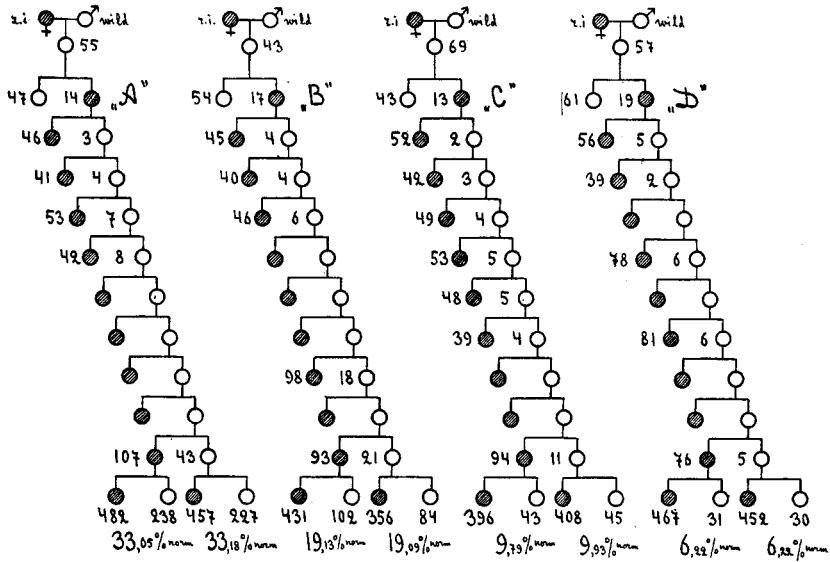
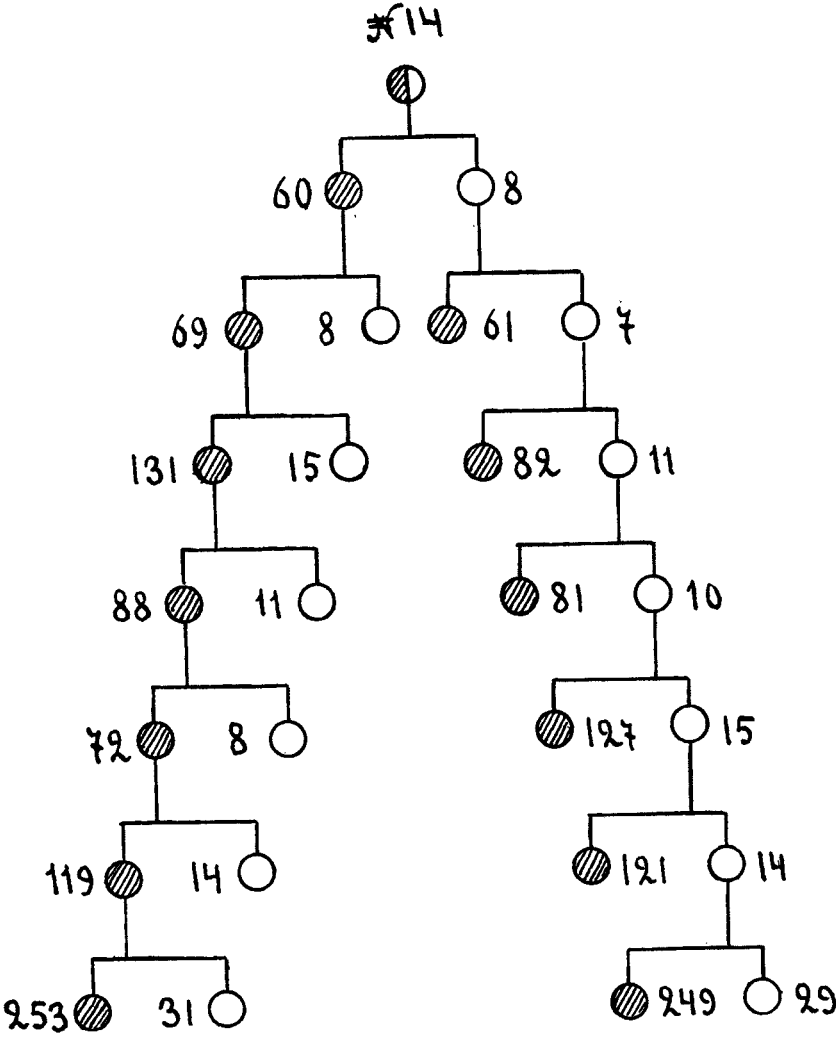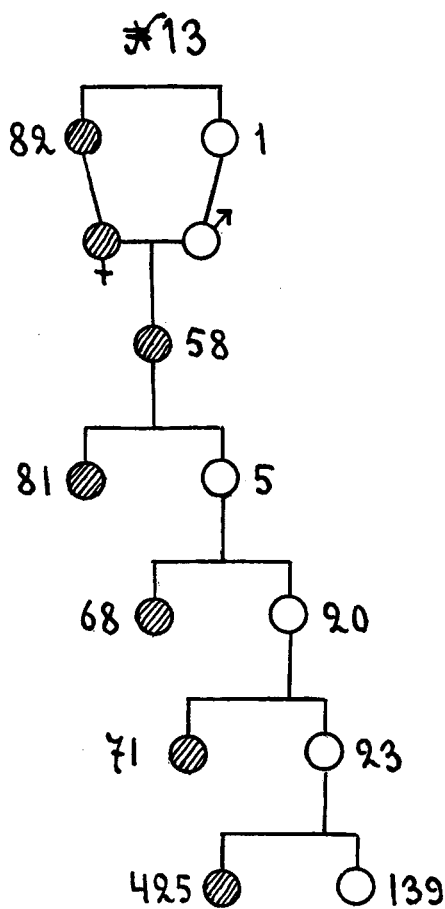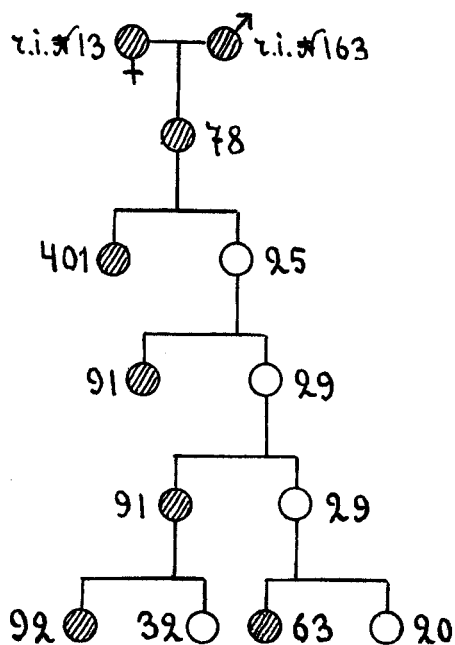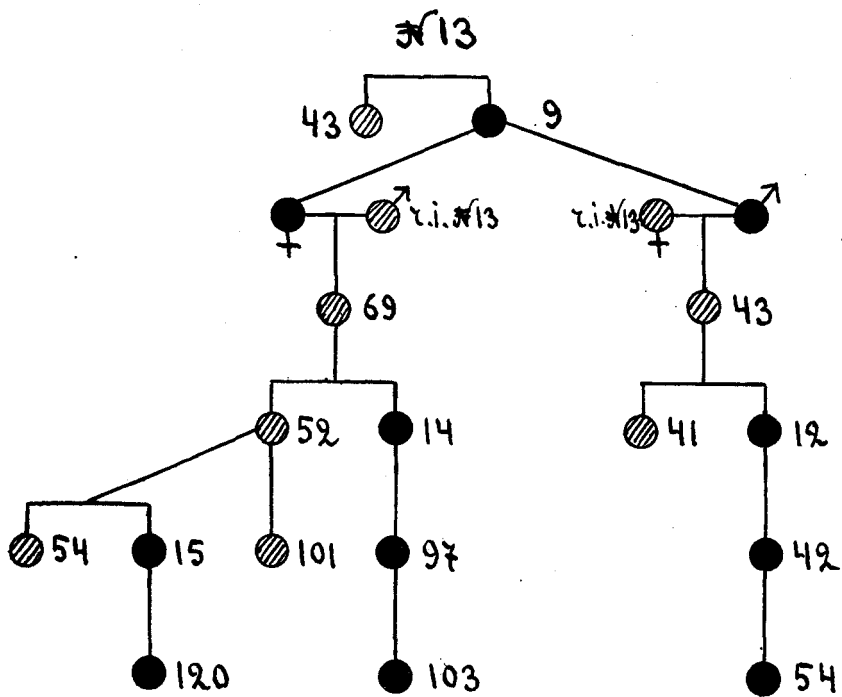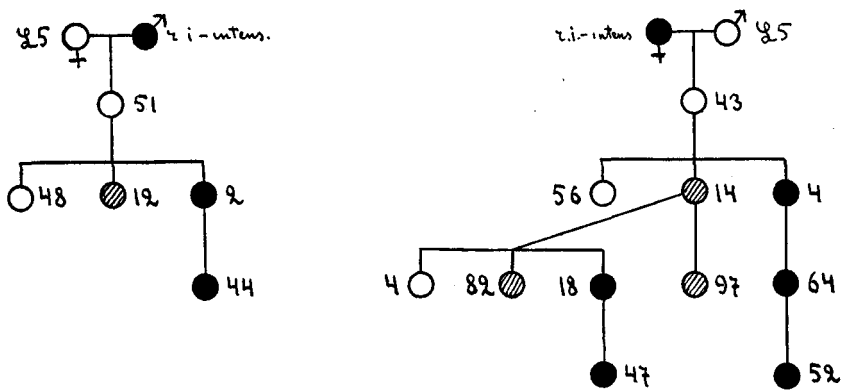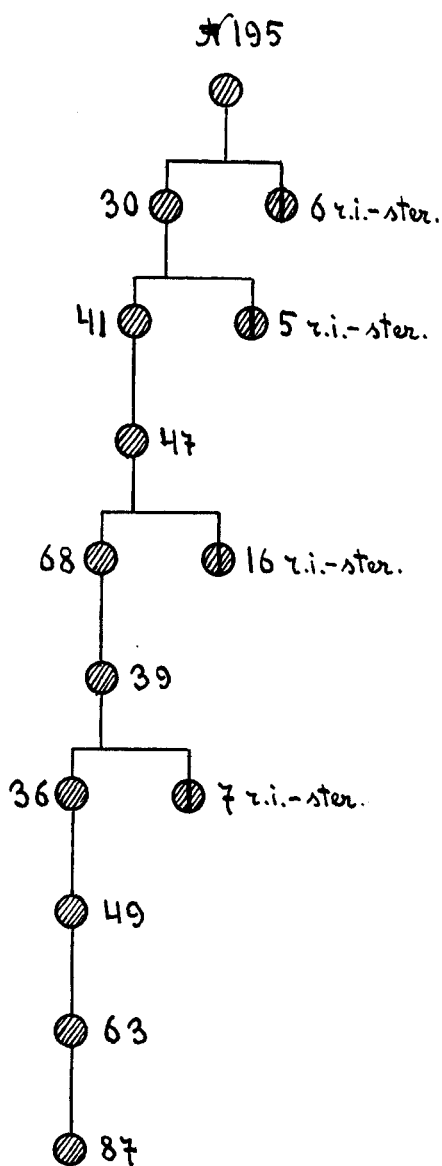DIAGRAM 7
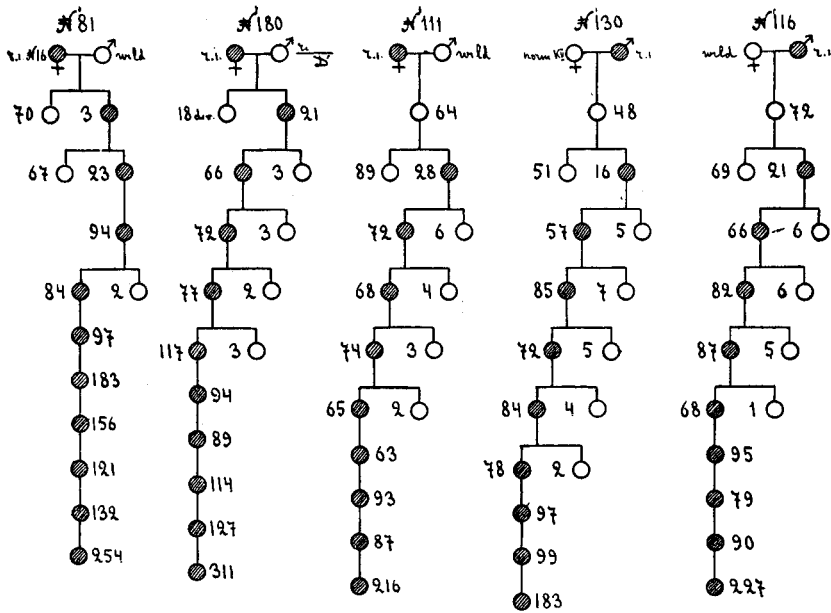
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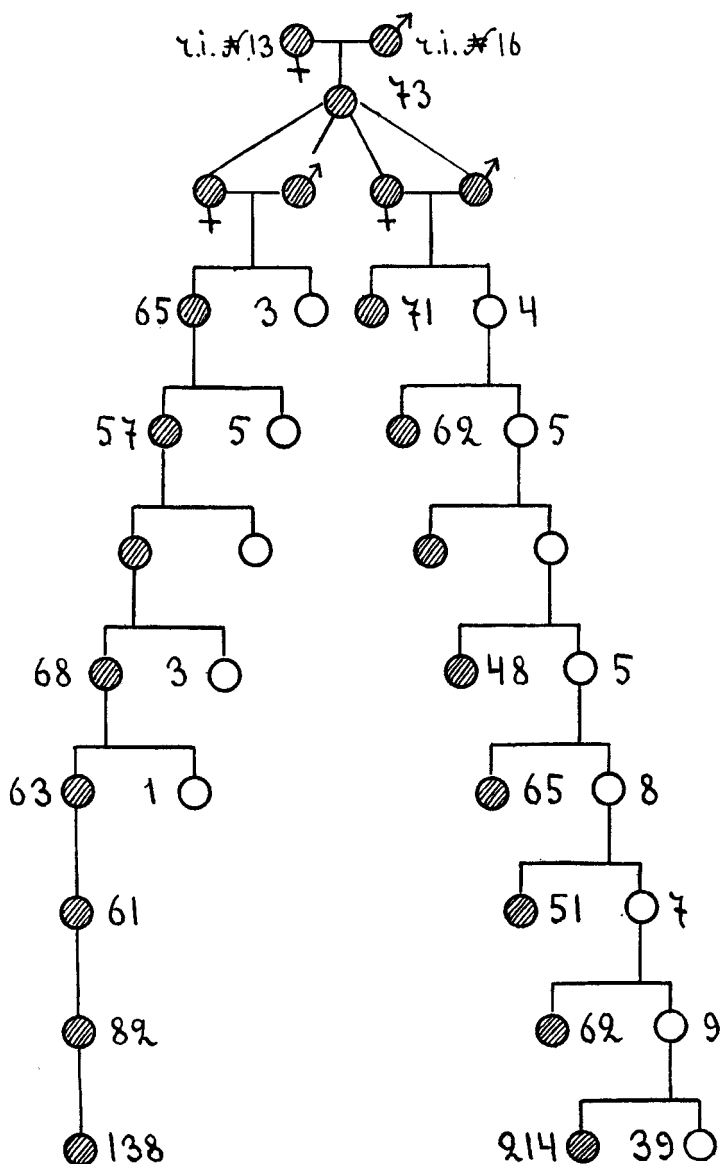
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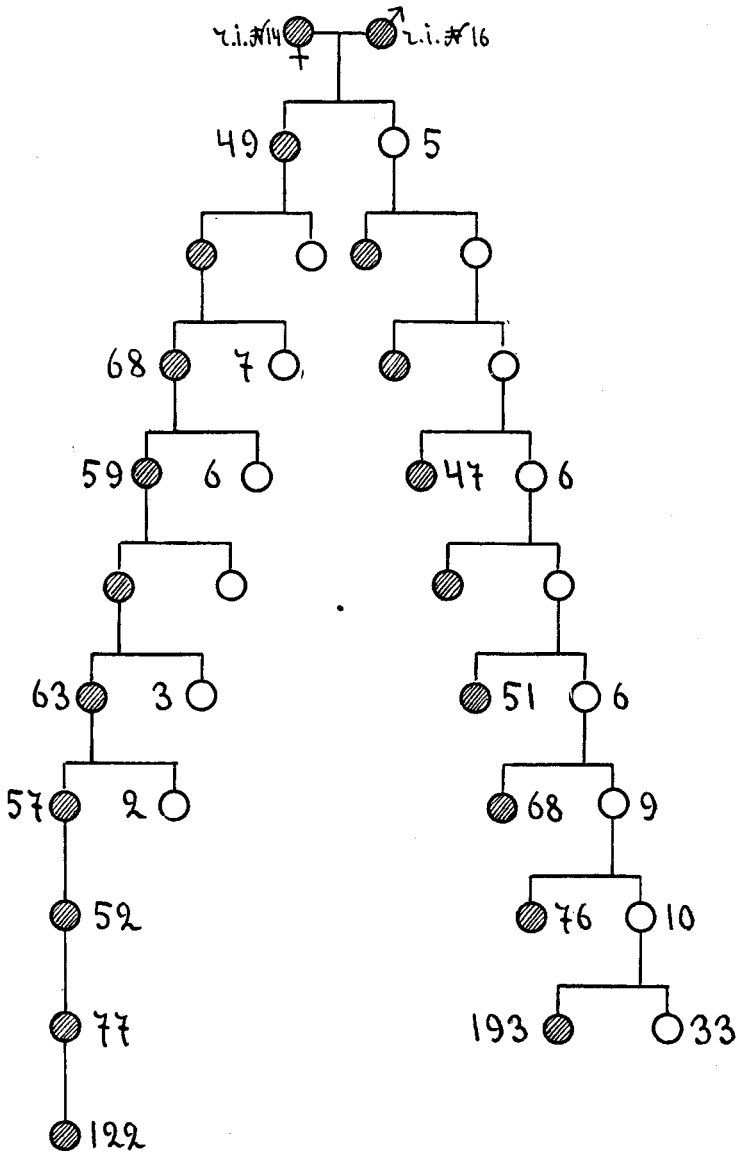
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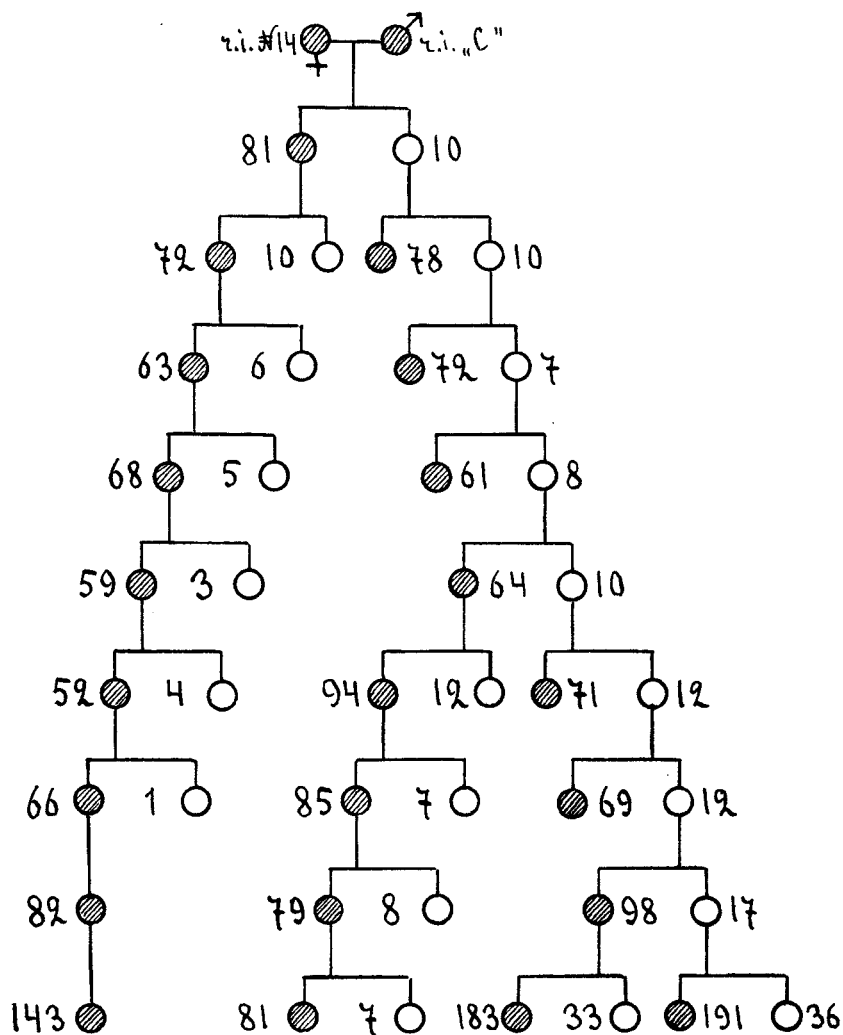
DIAGRAM 11

DIAGRAM 12

DIAGRAM 13

DIAGRAM 14

DIAGRAM 15

DIAGRAM 16

DIAGRAM 17

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DIAGRAM 18

DIAGRAM 19

DIAGRAM 20